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Oviposition Behaviour of the Jack-pine Sawfly, *Neodiprion americanus banksianae* Roh., as Indicated by an Analysis of Egg Clusters[1]

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Introduction

This study was undertaken as part of a broader investigation of the behaviour of the jack-pine sawfly, *Neodiprion americanus banksianae* Roh. The greater part of the investigation was directed towards an understanding of larval group-feeding behaviour, but in order to clarify the situation in which this insect begins larval life, large numbers of egg clusters were analysed with special attention paid to the positional relations of egg-bearing needles. Such analysis has permitted certain inferences on the oviposition behaviour of this insect and this indirect information is of value in view of the difficulties experienced in efforts to induce this species to oviposit under laboratory conditions for direct observation. Fortunately, egg clusters obtained from the field are well adapted to descriptive measurement and analysis, for in order to lay its full complement of eggs the adult female sawfly must select as many as 20 to 30 needles, thus leaving behind it a readily measured record of its egg-laying behaviour.

A typical egg cluster of the jack-pine sawfly is shown in Fig. 1. This species overwinters in the egg stage; the larvae appear in late spring and feed on mature foliage of the previous year. Male and female larvae pass through four and five feeding instars respectively during development. Shortly after moulting to a fifth or sixth non-feeding prepupal instar, the larvae spin cocoons. Emerging from these cocoons during late summer, the adults mate and the eggs are laid on the mature foliage of the current year. Each egg is deposited in a slit cut into the needle edge by the saw-like ovipositor of the adult female sawfly. Each needle selected for oviposition usually bears a series of such egg-slits spaced at more or less regular intervals.

Methods and Materials

The majority of the egg clusters examined in this study were obtained on Cloche Island in the North Channel, north of Manitoulin Island, Ontario. The remainder were collected either at Point aux Pins near Sault Ste. Marie, or in the vicinity of the Petawawa Forest Experiment Station at Chalk River, Ontario.

The needles of the jack pine, *Pinus Banksiana* Lamb., are paired, the needle pairs being arranged on the shoot in confluent spirals. For egg-cluster analysis, it was desired to observe and remove each pair in order from the base to the tip of the shoot. This was found to be most readily accomplished by holding the base of the shoot in the left hand, with the tip away from the observer, and in this position rolling the shoot clockwise between the fingers. Using this pro-

[1]Based on part of a thesis submitted to the University of Toronto in partial fulfilment of the requirements for the degree of Master of Arts. Data for this paper were gathered during studies of the jack pine sawfly, conducted at the Department of Zoology, Universiy of Toronto, and supported by a fellowship donated by the Spruce Falls Power and Paper Co., and by a Research Council of Ontario Scholarship.

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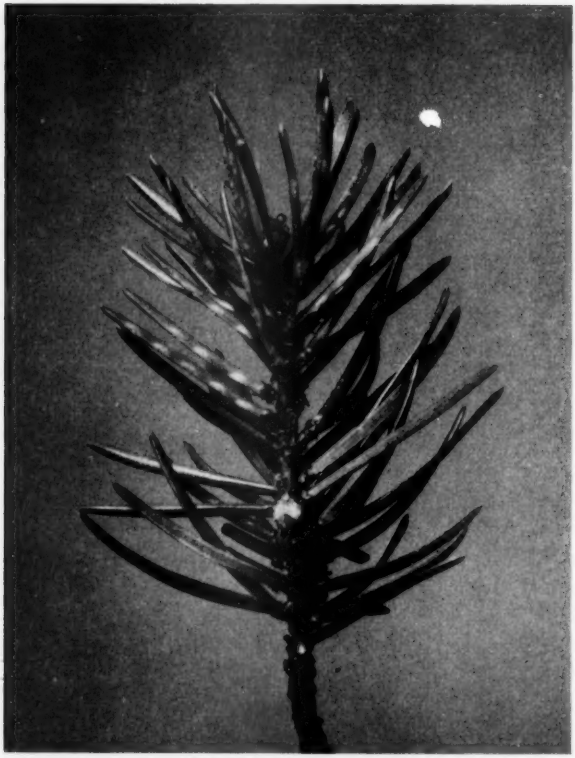

Fig. 1. A typical egg cluster of the jack-pine sawfly, *N. a. banksianae* Roh. Photograph by D. C. Anderson.

cedure, a quarter to a half turn suffices to bring up each time the next lowest needle pair for observation and removal.

Holding the shoot as described, each needle pair may be considered as being composed of a *right* and a *left* needle. Each needle in turn may be described as having a *curved* and a *flat* surface, and, where these meet, *apical* and *basal* edges towards the tip and base of the shoot. Fig. 2 illustrates these features.

Egg-cluster descriptions were taken in the following manner. The length of the foliated portion of the shoot was recorded. Holding and rotating the shoot as described, the needle pairs between the base of the shoot and the first needle pair bearing eggs were counted. Within the egg cluster itself, as delimited by the lowermost and uppermost needle pairs bearing eggs, all needle pairs, with or without eggs, were tallied in consecutive order. For egg-bearing needles, the number and position of the eggs with respect to needle and edge were tallied. Finally, the number of apical, blank needle pairs was recorded. In this way a sequential tally of the egg distribution was obtained.

From within each egg cluster, a sample of 20 to 30 needles was preserved for measurement of needle length. Occasional aborted needles markedly shorter than the rest were omitted, since these were never observed to bear eggs.

From Fig. 1 it can be appreciated that an egg cluster consists of a group of needles, each bearing along one or the other edge a portion of the total complement of eggs. Apical and basal edges of right and left needles of each needle pair present four possible sites for oviposition. In order to analyse the data for preferential selection within these four sites, it was necessary to bear in mind that such preference might be expressed either by greater numbers of a particular site being selected for oviposition, or by a greater number of eggs being laid in a particular site whenever it was selected. Preliminary analysis eliminated the latter possibility. Within the accumulated egg distributions of 32 clusters it was found that the mean, the range, and the shape of egg distributions for these four sites were virtually identical. Further analysis for preferential selection of oviposition sites therefore proceeded with reference only to the incidence of selection of the sites, without regard to the number of eggs laid in each instance.

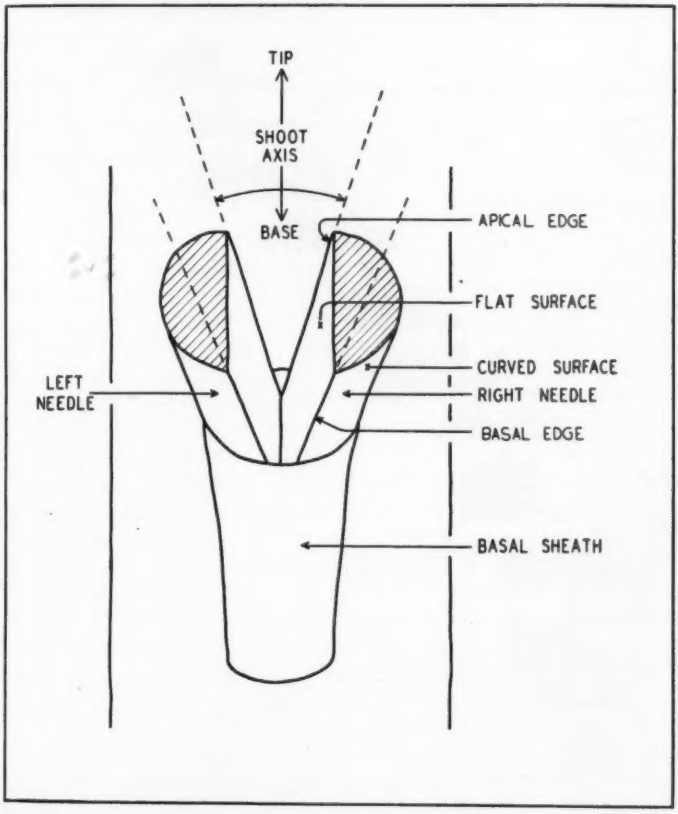

Fig. 2. Cross-section of a pair of jack pine needles cut just above the basal sheath, showing the location of edges and surfaces to which reference is made in the text. The orientation of the needle pair with respect to the shoot is such that the shoot axis bisects the angle described by opposed flat surfaces of adjacent needles. This orientation permits the needles of a pair to be classified as *right* and *left* needles.

Results

Location of the cluster on the shoot

Counts of the number of needle pairs from the base of the shoot to the first needle pair bearing eggs and from the last needle pair bearing eggs to the tip of the shoot were made for 96 clusters. These data were arranged for a paired "t" test by subtracting the number of apical from the number of basal blank needle pairs. A mean difference of 20.2 needle pairs favouring the location of the cluster towards the tip of the shoot yielded a "t" value of 8.48, which, with 95 degrees of freedom, greatly exceeded the "t" value required at the .001 level of significance.

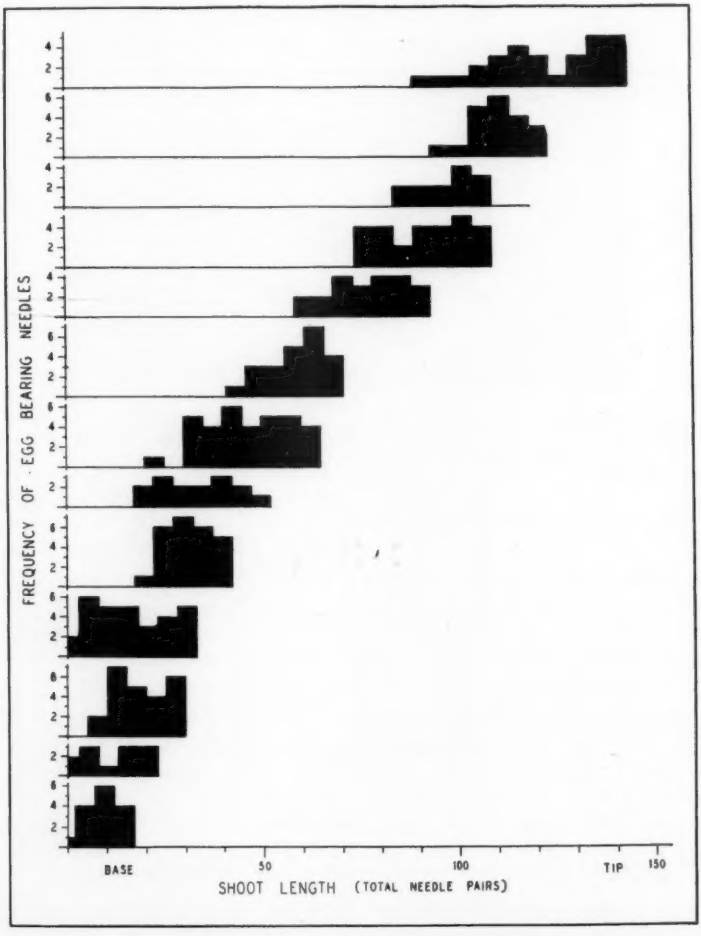

Fig. 3. Location of jack-pine sawfly eggs in 13 clusters selected to represent a graded series of shoot lengths, as measured by the total number of needle pairs on the shoot. Histogram bars indicate the number of needles bearing eggs within consecutive sets of five needle pairs.

This selection of the apical end of the shoot is depicted in Fig. 3. In the preparation of this figure, shoots were selected with reference only to the total number of needle pairs on the shoot, regardless of the position of the clusters. It is at once apparent that "cluster" is a valid term. Moreover, it can be appreciated from this figure that the probability value obtained in the "t" test is in no way extreme, for its strength is dependent entirely upon the length of the shoots used in the analysis. Except in extremely short shoots that coincide with the normal length of the cluster itself, the cluster tends to occupy a relatively constant number of needle pairs at the apical end of the shoot.

Oviposition on right and left needles

Data on 118 clusters permitted comparison of the incidence of oviposition on *left*, as against *right*, needles of the needle pair. Subtracting the number of *right* from the number of *left* needles bearing eggs for each of the 118 clusters, yielded an average positive difference of only 0.17, and a "t" value of 0.398 with 117 degrees of freedom. The probability value of .69 thus obtained agrees with the inference that females would show no preference for *right* or *left* needles.

Oviposition on apical and basal edges

Data on 119 clusters were used in comparing the incidence of oviposition on the apical as against the basal edges of the needles. A paired "t" test was performed by subtracting in each cluster the number of needles bearing eggs on their apical edge from those bearing eggs on their basal edge. Basal-edge laying was found to predominate in 103 of the 119 clusters, and the "t" value of 9.09, with 118 degrees of freedom, indicated a probability greatly in excess of the .001 level of significance.

More detailed examination of the proportion of basal-edge laying within each of the clusters indicated that, although basal-edge laying greatly predominated, the directive factors responsible were evidently open to gradual modification, even to the point of complete reversal. A few clusters, otherwise normal in terms of total eggs and total occupied needles, were comprised almost entirely of needles bearing eggs on their apical edges. It seemed advisable to repeat the study on material collected in such a way that the gravitational relations of the needle edges could be assessed.

A protractor fitted with a free-swinging pendulum needle was used to measure the orientation of 33 egg clusters collected near the Petawawa Forest Experiment Station during the spring of 1954. In addition to recording the orientation of the shoot, the gravitational mid-point of the underside of each shoot was marked with a small pin before removing the shoots from the tree. In this way, it was possible to orientate each shoot on a pinning board at the same angle at which it had been borne on the tree.

Each egg-bearing needle was removed with fine scissors and its orientation with respect to gravity recorded. Of the 745 egg-bearing needles on the 33 clusters, 518 bore eggs on the basal edge of the needle and 227 on the apical edge. Of the 518 basal edges, 443 were the lower gravitational edges. In the same way, 201 of the 227 apical edges bearing eggs were on needles so orientated that the apical edge was the lower gravitational edge. There was, therefore, a total of 644 of the 745 needles which bore eggs on the lower gravitational edge. Of the remaining 101 needles, which bore eggs on the upper gravitational edge, many stood either almost straight up or straight down, so that neither edge was in reality a true gravitational lower edge.

These observations suggest that the greater stability assured by its weight being slung below the needle is of appreciable significance in the selection by a female of a needle edge for oviposition. The orientation of these shoots ranged from those that drooped as much as 60° below the horizontal, to those that stood at angles as great as 80° above. On those shoots that stood markedly above the horizontal, basal edges tended to be the lower gravitational edges of the majority of the needles. Conversely, on those less frequent shoots that drooped well below the horizontal, apical edges tended to be the lower gravitational edges of the majority of the needles. This feature accounts for the few complete reversals to apical-edge laying observed in the earlier analysis.

Oviposition on adjacent needles in a needle pair

Data from 80 clusters allowed analysis for evidence of discrimination during oviposition relative to the paired nature of jack pine needles. Within these 80 clusters, 390 needle pairs bore eggs on both needles, 1248 bore eggs on one needle of the pair only, and 918 were free of eggs. The total of 2556 needle pairs must be raised to include those blank needle pairs, immediately adjacent to the egg clusters, that were potential oviposition sites. Having taken the original limits of the cluster as the uppermost and lowermost needles bearing eggs, it can now be argued that if within the cluster a needle pair had a probability of 918/2556 of being blank, then the blank needle pairs immediately above and below the cluster had a similar chance of forming part of the cluster. In 111 of the 80 x 2, or 160, potential positions, additional needle pairs did occur above or below the uppermost or lowermost needle pair bearing eggs. In this way, 918/2556 x 111 or approximately 40 additional blank needle pairs must be accepted as belonging to the clusters.

Proceeding with the calculation of "p" and "q" values, there is a new total of (2556+40) x 2 or 5192 needles. Blank needle pairs now comprise (918+40) x 2, or 1916, blank needles. To these must be added one needle from each of the 1248 needle pairs in which only one needle bore eggs, giving a total of 3164 needles. The probability value "q" can now be calculated as 3164/5192 or .609. The value "p" is therefore .391.

A comparison of the observed incidence of the possible combinations of

TABLE I

A comparison of the observed incidence of the possible combinations of blank and egg-bearing needles among 2596 needle pairs, with the expected values derived from the expansion of $(p+q)^2$*.

Class	Fraction	EXPECTED	OBSERVED	Chi-square
Both needles bearing eggs (p^2)	.153	397	390	.123
One needle bearing eggs (2pq)	.476	1236	1248	.117
Neither needle bearing eggs (q^2)	.371	963	958	.026
			TOTAL CHI-SQUARE	0.266
			D. of F. = 1; P = 0.5 − 0.7	

* p = probability of a needle bearing eggs = .391
q = probability of a needle being blank = .609

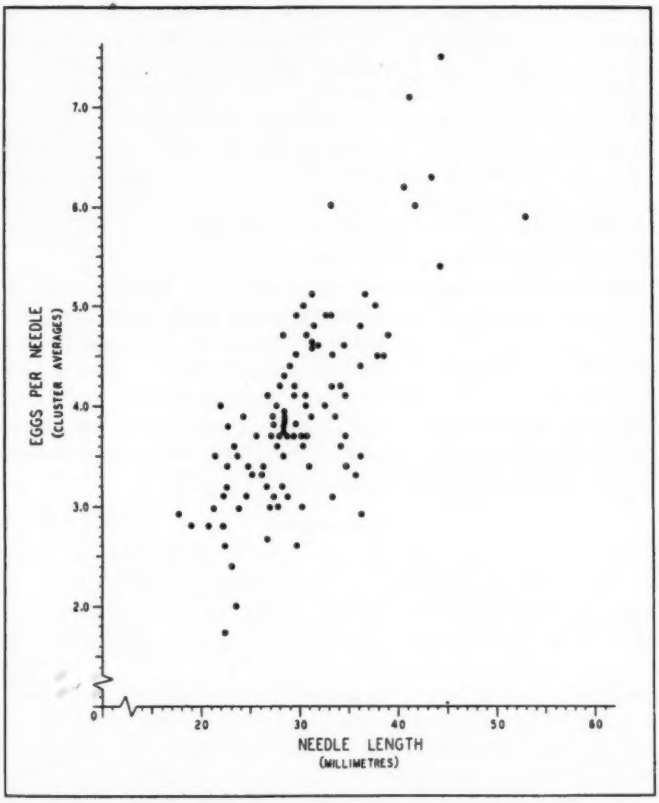

Fig. 4. Correlation diagram; eggs per needle v. needle length. Each point represents the average of egg counts from all egg-bearing needles in 101 clusters plotted against the average length of 20 to 30 needles from the same clusters. $r_{x.y} = +.627$.

blank and egg-bearing needles with expectation based on the expansion of $(p+q)^2$ is presented in Table 1. The agreement between observed and expected values is virtually perfect, and it is therefore concluded that oviposition on one needle of a pair does not influence the chances of the adjacent needle bearing eggs. These data furnish no evidence that the adult female sawfly is cognizant of the paired nature of jack pine needles.

Egg number in relation to needle length

Atwood and Peck (1) focused attention upon the number of eggs per needle as an aid to identification. Of the jack-pine sawfly they state: "This species usually lays three, four or five eggs per needle, . . . , although variations occur." Data gathered in this study afford an opportunity to assess the variation present and the degree to which it may be correlated with needle length.

Preliminary studies indicated that samples of as few as 15 needles per egg-cluster provide an adequate measure of average needle length, and that the distribution of egg numbers per needle within the cluster displays a strong

central tendency, so that the arithmetic mean for the cluster is a satisfactory representation of the distribution. Fig. 4 is a correlation diagram illustrating the strength of the relation found to exist between average egg number per needle and average needle length in 101 clusters. The evident correlation shown in this diagram is borne out by the correlation coefficient attained, $r_{x.y} = +.627 \pm .060$. For the 99 degrees of freedom available in this analysis, the .001 level of significance requires a correlation coefficient of only .322. Squaring the correlation coefficient indicates that approximately 40 per cent of the variation in average egg number per needle can be attributed to correlation with average needle length, 60 per cent remaining as the error component.

From the correlation diagram, it can be seen that the great majority of the clusters fit in the range of three to five eggs per needle given by Atwood and Peck (1). At the same time, the observer should not be surprised to find very short-needled shoots averaging two or less eggs per needle, nor very long-needled shoots averaging as many as seven or more eggs per needle.

It is probable that variation in egg spacing accounts for a substantial portion of the error component, so that it might be expected that a consideration of egg spacing would have strengthened the correlation.

Discussion

The foregoing analyses may now be considered in relation to the overall picture of oviposition they present. "Egg cluster" is evidently a valid term, these clusters tending to occupy a more or less restricted area towards the tip of the shoot. Whatever the reactions involved, they are apparently effective in localizing the movements of the adult female sawfly during oviposition. Some reaction must be initially responsible for the female assuming a position near the tip of the shoot, and it is probable that this reaction holds it within an inch or so of the tip during oviposition. Once oviposition begins, the odour of lacerated needles may also serve to restrict the wanderings of the female, and may, in some instances, serve to attract a second female to the same shoot. Some such explanation is almost necessitated by the very large clusters occasionally observed. Of the 109 egg clusters analysed from the Cloche Island Collection, 96 bore less than 130 eggs. Of the remaining clusters, however, some were very large. For example, one cluster bore 262 eggs on 68 needles, while another bore 317 eggs on 77 needles. Clusters of this size may represent the work of three or more sawflies.

After selecting the needles towards the tip of the shoot, the adult female seemingly makes no further distinction between needles within this area. Right and left needles of a pair are used at random; and both, one, or neither of the needles of a pair bear eggs in almost exactly the ratio predicted by the binomial theorem. In this respect the behaviour of *N. swainei* Midd. is noteworthy. Atwood (2) describes this behaviour as follows: "Adult sawflies emerge from the cocoons in late June or early July. At this time, the young needles of the jack pine are about one inch long and two needles which grow from each sheath are still close together for their whole length. The slits for the reception of eggs are made in such a way that each pair of needles bears a pair of eggs placed opposite each other." In contrast, *banksianae* lays its eggs in late summer or early fall, by which time the foliage of the current year is mature. On these strongly divergent needles the oviposition behaviour of *banksianae* appears to be completely unaffected by the paired nature of jack pine needles, evidence

which strongly suggests that the adult female sawfly is not cognizant of their paired nature.

The correlation found between egg number and needle length suggests that this species is either weakly or not at all predisposed to lay any special number of eggs per needle, but simply continues to lay eggs so long as the particular length of needle permits. This observation suggests that what is effectively a characteristic egg-number for this species is so only by virtue of the relatively uniform length of jack pine needles.

The predominance of egg laying on the lower gravitational edge is of interest in relation to the rare occurrence of needles bearing eggs on both edges. At an early stage of this study, calculations were made on the number of such instances of "double oviposition" to be expected if they represented a mere random coincidence of the observed proportions of basal- and apical-edge laying. It was at once apparent that there were only one-tenth as many needles bearing eggs on both edges as would be expected from such a random association. Several of these rare needles with eggs on both edges were dead, evidently killed by the double set of lacerations. Since the lower gravitational edge is predisposed for selection where there is a marked contrast in the gravitational relations of the two edges, the consequent reduction in the incidence of double oviposition may be looked upon as a small, but nonetheless real, factor tending towards increased survival of the species.

Summary

The method of egg-cluster description used in this study is described. Egg clusters were located with highly significant regularity towards the tip of the shoot. Oviposition was independent of the paired nature of jack pine needles, no preference being shown for *right* or *left* needles of the needle pair, and both, one, or neither of the needles of a pair bearing eggs in almost exactly the ratio predicted by the binomial theorem. Oviposition on the *basal* edges of the needles predominated. This predominance arises from a strong preference for the lower gravitational edge of the needle, a preference satisfied by the *basal* edges of needles on the great majority of jack pine shoots which are orientated at angles above the horizontal. Egg number per needle was found to bear a strong positive correlation with needle length, suggesting that what is effectively a characteristic egg number per needle for the species arises from the narrowly limited variation in the length of jack pine needles.

Acknowledgments

The author wishes to express his indebtedness for advice received from many associates during the conduct of this study and the preparation of the manuscript, particularly J. R. Dymond, C. E. Atwood, and L. Butler, Department of Zoology, University of Toronto, and M. L. Prebble and R. M. Belyea, Forest Biology Division, Department of Agriculture.

Egg collections were provided in 1950 by C. E. Atwood, and in 1952 by E. O. Clinton, Forest Insect Laboratory, Sault Ste. Marie, Ont. Figs. 2, 3, and 4 were prepared by Miss P. M. G. West of the Forest Insect Laboratory.

Nomenclature

Neodiprion americanus banksianae Roh. is given as the specific name of the jack-pine sawfly by Ross (3) "Hymenoptera of America North of Mexico" p. 20. Before this catalogue was published in 1951 this insect was known as *N. banksianae* Roh.

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Note on Injury to Tree Fruits by *Frankliniella tritici* (Fitch) (Thysanoptera: Thripidae)[1]

By H. R. Boyce[2]
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The thrips *Frankliniella tritici* (Fitch) occurred in great abundance early in May, 1954, in orchards of tree fruits in Essex County, Ontario.

Observations during the first three weeks of May showed that this insect was abundant on the foliage and blossoms of apple, sweet and sour cherries, plum, and peach. Sweet cherry, European plum, and peach suffered the greatest attack. On sweet cherry and plum large numbers of eggs were inserted in blossom stems, styles and apices of the ovaries. From 30 to 50 per cent of the blossoms of sweet cherry and plum were destroyed, apparently because of disruption of tender tissues by the large numbers of eggs inserted in them; a considerable number of the fruits remaining on the trees were injured by feeding of adults and immature stages of the thrips (Fig. 1).

Fig. 1. Injury to sweet cherry fruits by *F. tritici.* Normal fruit on right.

On peach, eggs were laid very freely beneath the epidermis of stems and receptacles of the developing fruit and frequently were found in groups (Fig. 2). Up to 35 eggs were deposited in various parts of a blossom. Although a few blossoms shrivelled and dropped, the injury did not appear to be of economic importance.

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Fig. 2. Group of eggs of *F. tritici* inserted under epidermis of stem of peach blossom.

According to Treherne (1923), Parrott, in 1909, noted extreme injury by *F. tritici* to pear orchards in western New York State. In 1937, Twinn (p. 82) reported a heavy infestation of strawberry plantations at Forest, Ontario, by this thrips. It appears that the present record constitutes the first instance of appreciable damage to tree fruits in Canada by *F. tritici.*

The specimens were identified by Mr. W. R. Richards, Entomology Division, Ottawa.

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Aphomia gularis (Zeller) (Lepidoptera, Pyralidae) at Baie d'Urfé, Quebec

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This moth was first reported on this continent as a pest in a consignment of peanuts, received in California from China (de Ong, 1919). Mr. Hahn W. Capps, of the United States Department of Agriculture, informs me, *in litt.*, that 6 adults from that infestation, together with 2 from "near prunes" in 1930, and 8 from a prune warehouse in 1931, at San José, are in the U.S. National Museum.

Wakely (1932) first recorded its occurrence in Britain. Jacobs (1934-35) has described its life-history and given a short history of its appearance in Europe. Hinton (1943) has described the larva in detail. Corbet and Tams (1943) described the facies of male and female adults, with photographs, and illustrated the genitalia. They also stated that its distribution is "India, China, and Japan, but found occasionally in Britain, Europe and North America." Its larval food appears to be limited to seeds, flour, nuts, and dried fruits. There are two specimens in the Canadian National Collection (Dr. E. G. Munroe, *in litt.*) reared

in 1934 from walnuts from a warehouse in Montreal. MacNay (1952, 1954) has also recorded the occurrence of this moth in a warehouse in Vancouver, B.C., in 1952.

A slightly rubbed specimen of this species entered an ultra-violet light-trap in the author's garden between 9.00 and 10.30 p.m. on 18 July 1953, along with about 100 gm. of other insects, mainly Trichoptera. The trap was situated on a terrace, facing south, about 300 feet from the Ottawa River. There are no warehouses nearer than those at Montreal, about 24 miles away eastwards. The specimen was identified by Dr. E. G. Munroe, Division of Entomology, Science Service, Department of Agriculture, Ottawa, Ontario, and has been deposited in the Canadian National Collection.

In view of the possibility that the moth may become established here, a description of the captured specimen might be useful. The right fore wing measures 10.5 mm. long and 3.0 mm. broad; the body with head, from the frons to the anal tip, is about 10.5 mm. long. Colour, by daylight: fore wings light yellowish brown ("beige"), the whole facies satiny, with a postmedium ("cell-end" of Corbet and Tams) brown dot circled by a light area; the light streak shown by Corbet and Tams, pl. IV, fig. 9, may have become eroded by contact with the other insects in the collecting jar; there is a distinctly lighter sublunate subterminal transverse band, narrowing at the tornus, with the veins and interspatial folds well-defined. Hind wings lighter. Below, the wings are of the same colour as the upper side of the hind wings. The thorax, abdomen and legs are concolorous with the basic colour of the fore wings; the edges of the abdominal segments below are light brown. The abdomen does not have the oily brown appearance commonly seen in moths whose larvae feed on nuts or on oil-bearing plants such as reeds.

The writer thanks Dr. N. D. Riley, Department of Entomology, British Museum (Nat. Hist.), London, England, for guidance to the essential literature, and Dr. Eugene Munroe for the references to captures in this country.

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Phytophaga tumidosae (Felt) (Diptera: Itonididae) and its Hymenopterous Parasites Reared from the Scarred Gall of Willow

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On February 13, 1954 a heavy infestation of small galls was noted on a growth of willow shrubs (*Salix* sp.) in London Township about a mile north of London, Ontario. The exact location was on the north bank of the North Branch of the Thames River about 100 yards west of the bridge by which Adelaide Street crosses the river. The bushes were crowded along the bank and several of them had their lower branches under water and their roots extending well out into the mud of the river. The galls were one-eighth to three-eighths of an inch long (Fig. 1) and were roughly spherical to oval in shape. The bark of a gall was scarred by shallow furrows running along its length. At its upper end each gall bore the scales of a withered bud or an oval scar from which the scales had fallen. Flanking the scar were two rounded swellings of incipient buds. Many of the galls were separately developed along the twigs, being well apart from one another, but in some cases they were crowded against one another so that three or four galls occupied one inch of the length of the twig, and in several instances a number of adjacent galls had coalesced to form an irregular swelling one or two inches long, along the length of a twig. In the key to insect galls of willow in Felt (1940) the galls were identified as scarred willow galls caused by the gall fly *Phytophaga tumidosae* (Felt).

Methods of Rearing

Two hundred and twenty-five galls were clipped from the twigs on February 13, 1954, care being taken to remove only galls which were separately developed. Twenty-five of the galls were opened and their contents examined. The bark of a gall was thin and the bulk of the gall was composed of yellow-green, sap-filled pith (Fig. 2). In this pith were tunnels which extended to the bark of the gall but did not pierce it. Consequently each tunnel was closed by a thin layer of bark at its outer end. In each tunnel was an orange itonidid larva about 3 mm. long, or a small hymenopterous larva, with its anterior end toward the opening of the tunnel. The anterior end of an itonidid larva was recognizable by the presence on it of the "breastplate" typical of larvae of the family Itonididae. Of the 25 galls opened, 10 contained one larva, 8 contained two larvae, 5 contained three larvae and 2 contained four larvae. The smaller galls contained one or two larvae and the larger ones three or four larvae.

Two hundred intact galls were prepared for the rearing of insects from them. Each gall was put in a separate, numbered glass vial of dimensions 60 mm. x 15 mm., plugged with cotton. The vials were kept on a rack and were examined daily for the presence of insects which had emerged from the galls. The insects were killed, pinned and labelled to show the date of their emergence and the number of the gall from which each insect had emerged. On September 10, 1954 the galls were discarded. All specimens reared from the galls are deposited in the Canadian National Collection except one specimen of *Phytophaga tumidosae* (Felt) retained in the collection of the University of Western Ontario. The specimens of *Phytophaga tumidosae* were kindly identified by Mr. J. F. McAlpine, Systematic Unit, Department of Agriculture, Ottawa and all the parasitic wasps were identified by Dr. O. Peck of the same organization. The numbers of the

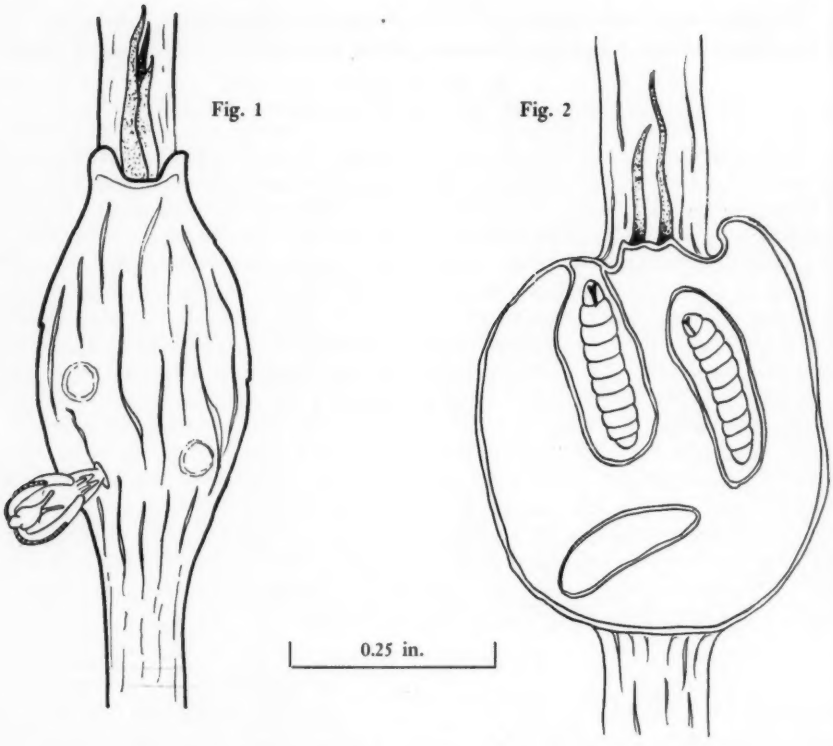

Fig. 1. Scarred gall on willow twig with empty pupa of *Phytophaga tumidosae* projecting from it.

Fig. 2. Scarred gall in longitudinal section, with larvae of *Phytophaga tumidosae* in two of the tunnels.

various species of insects that emerged from the galls, and their dates of emergence, are recorded in Table 1.

Account of Insects Reared

During the period March 1 to June 15, 1954 one hundred and forty insects emerged from 84 of the 200 galls. Of these 84 galls 3 yielded one specimen of *Phytophaga tumidosae* (Felt) each, 46 yielded one parasitic wasp, 21 yielded two wasps, 8 yielded three wasps, 5 yielded four wasps and 1 yielded five wasps each. Thus, only three of the 84 galls yielded specimens of the fly, *Phytophaga tumidosae*, which caused the galls, while 81 (96%) were parasitized by wasps.

Diptera

Itonididae

Phytophaga tumidosae (Felt)

Three flies of this species emerged from three galls, one male on March 13, one female on March 1 and one female on March 4. The latter specimen is deposited in the collection of the University of Western Ontario. Each insect,

TABLE I

Insects reared from Scarred Galls of Willow

Date	Insects Reared								
	Phytophaga tumidosae	*Tetrastichus* sp. (near *rosae*)	*Tetrastichus* sp. (near *semiauratiiceps*)	*Torymus* sp. (near *coloradensis*)	*Torymus* sp. (near *thalassinus*)	*Torymus* sp.	*Eurytoma* sp. (near *diastrophi*)	*Platygaster* sp. (near *astericola*)	Total
March 1	1	2							3
2		10							10
3		8							8
4	1	10							11
5		12						6	18
6		8						4	12
7		11						6	17
8		4					1	4	9
9		1					1	6	8
10		4					1	2	7
11		2						2	4
12		1						3	4
13	1	2						3	6
14								1	1
15								1	1
17		1						1	2
18							1		1
20								5	5
26							1		1
April 22							3		3
May 3			1						1
4							1		1
6							1		1
15		1		1					2
17		1							1
18							1		1
25						1			1
June 15					1				1
Totals	3	78	1	1	1	1	11	44	140

in its pupal stage, emerged from a gall through a hole about 0.5 mm. in diameter in the wall of the gall. The fly emerged from the pupa and left the empty pupal skin stuck by its posterior end in the hole (Fig. 1).

Hymenoptera

Eulophidae

***Tetrastichus* sp. (near *rosae* Ashmead)**

Seventy-eight wasps (including 40 males) identified as *Tetrastichus* sp. (near *rosae* Ashmead) emerged from 57 of the galls between March 1 and May 17 with the maximum number, 12, emerging on March 5 (Table 1). In most cases only one or two wasps emerged from a single gall but two galls yielded three wasps and one yielded four wasps. Peck (1951) lists several species of *Tetrastichus* as parasites of insect galls and includes *T. rosae* as a parasite particularly of galls caused by cynipid wasps of the genus *Diplolepis*. Judd (1953) reared wasps of the genus *Tetrastichus* from the willow gall caused by the gall fly *Rhabdophaga strobiloides* in the vicinity of London.

***Tetrastichus* sp. (near *semiauraticeps* (Girault))**

One wasp, identified as *Tetrastichus* sp. (near *semiauraticeps* (Girault)), emerged from a gall on May 3. Peck (1951) lists *T. semiauraticeps* as being reared from galls on *Pinus*.

Torymidae

***Torymus* sp. (near *coloradensis* (Huber))**

A single female wasp, identified as *Torymus* sp. (near *coloradensis* (Huber)), emerged from a gall on May 15 and was the only insect that emerged from that gall. Peck (1951) records that wasps of the genus *Torymus* are usually associated with plant galls and that *T. coloradensis* is a parasite of itonidid galls. Thompson (1950) lists many species of *Callimome* (=*Torymus*) as parasites of insect galls. Judd (1953) reared *Torymus* spp. from willow galls caused by *Rhabdophaga strobiloides* in the vicinity of London.

***Torymus* sp. (near *thalassinus* (Crosby))**

A single female, identified as *Torymus* sp. (near *thalassinus* (Crosby)), emerged on June 15 from a gall that had previously yielded one specimen of *Tetrastichus* sp. (near *rosae*) on March 2. Thompson (1950) and Peck (1951) list *T. thalassinus* as reared from galls caused by *Harmolita* sp. on grass.

***Torymus* sp.**

A single male, identified as *Torymus* sp., emerged on May 25 from a gall and was the only insect that emerged from that gall.

Eurytomidae

***Eurytoma* sp. (near *diastrophi* Walsh)**

Eleven wasps, identified as *Eurytoma* sp. (near *diastrophi* Walsh), emerged between March 8 and May 18 from nine galls (Table 1). Five of these galls yielded only *Eurytoma* sp., three galls yielded *Tetrastichus* sp. (near *rosae*) or *Platygaster* sp. (near *astericola* (Ashmead)) as well as *Eurytoma* sp., and one gall yielded all three parasites, *Eurytoma* sp., *Platygaster* sp. and *Tetrastichus* sp. (near *rosae*). Thompson (1950) and Peck (1951) list several galls as hosts of wasps of the genus *Eurytoma* and Judd (1954) reared *Eurytoma* sp. from willow galls caused by the saw-fly *Euura salicis-nodus* (Dalla Torre) in the vicinity of London.

Platygasteridae

***Platygaster* sp. (near *astericola* (Ashmead))**

During the period March 5-20 forty-four wasps, identified as *Platygaster* sp. (near *astericola* (Ashmead)), emerged from 23 galls (Table 1). Several of these galls yielded only *Platygaster* sp. but many yielded also *Tetrastichus* sp. (near *rosae*) and *Eurytoma* sp. (near *diastrophi*). Thompson (1950) and Peck (1951) list several species of *Platygaster* as parasites of insect galls. *P. astericola* is a parasite of an itonidid gall on *Aster* (Peck, 1951).

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Identity of a Cottony Scale on Peach in Ontario[1]

By J. H. H. PHILLIPS[2]
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Severe local infestations of a cottony scale on peach have been reported from the Niagara district of Ontario since the early 1920's. The species has been commonly referred to the cottony peach scale, *Pulvinaria amygdali* Ckll., but Steinweden (1946) showed that *amygdali* was an entirely different species, leaving the identity of the local species on peach in doubt.

In 1949, in a communication to Mr. W. L. Putman of the Vineland Station laboratory, Steinweden identified local specimens as being near *P. occidentalis* Ckll. He had previously expressed the opinion, however (Steinweden, 1946), that *occidentalis* may be the same as the species known in Europe as *P. vitis* (L.).

In 1954, specimens of this scale from peach in the Niagara Peninsula were submitted to Dr. D. J. Williams of the British Museum (Nat. Hist.), who (in litt.) expressed the opinion that there was little justification for the separation of this species from *P. vitis* as known in Europe.

Comparison of the scale from peach in Ontario with specimens accepted as of *P. vitis* from both England and Germany confirmed Dr. Williams' opinion that the local scale is very near to this species. Limited host studies indicate also that the cottony scale hitherto reported only on peach and plum in Ontario may have a wider host range, similar to that reported for *P. vitis*.

Reference

Steinweden, J. B. 1946. The identity of certain common American species of *Pulvinaria* (Homoptera: Coccoidea: Coccidae). *Microentomology* 11: 1-28.

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Rates of Oviposition of *Tribolium confusum* Duv. (Coleoptera: Tenebrionidae) Surviving Exposure to Residues of *p-p'*-DDT[1]

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Stored Product Insect Unit, Entomology Division Ottawa, Canada

The use of residual insecticides is increasing in insect control programs. In practice all insects do not receive lethal dosages, possibly because of uneven application of insecticide and the failure of some insects to come in contact with treated surfaces. This study was designed to determine the rate of oviposition of adult females of *Tribolium confusum* Duv. surviving exposure to DDT residues and to compare this rate with that of unexposed females.

The effect of insecticides on oviposition has been demonstrated with other species by several workers. Plumner and Baker (1946) found that specimens of the Mexican fruit fly, *Anastrepha ludens* (Loew), that had ingested food containing sublethal doses of tartar emetic laid significantly fewer eggs than those not given this material. Tenhet (1947) found that test insects of the cigarette beetle, *Lasioderma serricorne* (F.), that had survived exposure to sublethal dosages of pyrethrum oil spray consistently deposited fewer eggs than untreated beetles. Kennedy (1946) observed that mosquitos exposed to sublethal dosages of DDT showed all the symptoms up to and including knockdown, yet the affected mosquitoes recovered within 24 hours and lived in apparent health for a further 48 hours at least.

Methods

Males and females of *T. confusum* were separated in the pupal stage (Park, 1934) and kept separately in a culture medium of 95 per cent second patent flour and 5 per cent wheat germ by weight (Loschiavo, 1952). Three weeks after emergence the males were placed ventral surface down over the pores of a seed-counting head of the type used to count timothy grass seed under vacuum. While being held in this position they were marked on the dorsal surface of the hind wings with gold enamel paint applied with an extremely fine camel's-hair brush. When the paint was dry the vacuum was turned off and the insects were placed in food receptacles with unmarked females of the same age. The insects were kept in a volume of food sufficient to prevent crowding as tests at 32°C. and 75 per cent relative humidity showed that females laid significantly fewer eggs where the amount of food per insect was less than 4 gm. From test groups of equal numbers of males and females maintained at 32°C. and 75 per cent relative humidity the mean daily rate of oviposition before exposure was determined. Twenty-four hours before exposure the females were separated from the males and held without food, as preliminary work had shown that more uniform mortality was obtained after a period of starvation.

In the first series of tests, mated females one month old were arranged in three replicates of 25 each and exposed to residual deposits of *p-p'*-DDT (courtesy Naugatuck Chemicals, Elmira, Ontario) prepared from refined deodorized kerosene and acetone solutions in concentrations of 1, 3, 5, 10 and 25 per cent. The solutions were applied to sand-blasted glass plates 10 cm. square at 1 ml. per 100 sq. cm., a crystalline deposit remaining on the surfaces after drying. Plastic rings 2 cm. deep and 10 cm. in diameter were placed on the plates to confine the insects during exposure. Each group was exposed for two hours at 32°C. After

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exposure each group was placed in wide-mouthed glass jars containing food medium and maintained at 32°C. and 75 per cent relative humidity for seven days; then mortality was assessed. The survivors were introduced into jars of food containing an equal number of marked males and maintained at the above temperature and humidity for 19 days. During this period eggs were removed and counted every three days and the mean daily rate of oviposition per female was determined.

Further tests were conducted to determine the rate of oviposition of female survivors during the first few days after exposure. One male and one female were placed in each of 50 vials containing 8 gm. of food. After four days the females were separated and exposed to 5 per cent *p-p'*–DDT residues (from benzene solution) for one hour at 32°C. Each treated female was placed with an untreated male in a vial of fresh food at 32°C. and 75 per cent relative humidity. Untreated females were handled in a similar manner. Each day for 12 days the contents of each vial were examined for eggs, vials containing dead females being discarded. The daily rates of oviposition were calculated for both surviving and untreated females.

Results and Discussion

Table 1 shows that the rate of oviposition of females surviving exposure to 1, 3, or 5 per cent DDT was unaffected from the seventh to the twenty-sixth day after exposure. The mean daily rate of oviposition of these survivors during this period was 11.1 ± 0.14 eggs per female, while that of untreated females was 11.5 ± 0.24 eggs per female. The rate of oviposition of females surviving exposure to 10 or 25 per cent DDT was significantly lower than that of unexposed females. The mean daily rate of these survivors during the same period was 7.7 ± 0.17 eggs per female. The degree of mortality among beetles exposed to the different concentrations appeared to have no effect on the rate of oviposition of the survivors.

Fig. 1 shows that the difference in rate of oviposition between untreated and treated females declined markedly from the first to the fourth day and then levelled off from the fifth to the twelfth day. Analysis of variance showed that

TABLE I.

Mean mortalities of females (three replicates of 25 each) of *T. confusum* exposed to various concentrations of *p-p'*-DDT and mean daily rates of oviposition of survivors

Concentration %	Mortality 7th day	Eggs laid per female						Mean of Means*
		10	13	16	19	22	26	
1	9.3	10.88	11.36	10.68	9.84	10.40	10.20	10.56
3	13.3	11.78	11.46	12.25	11.79	11.37	11.67	11.72
5	18.3	10.02	11.11	12.65	11.49	9.95	10.34	10.92
10	20.0	8.19	7.34	8.39	7.31	7.10	6.36	7.45
25	22.0	7.55	8.55	8.85	8.66	7.58	6.25	7.91
Control	0	11.77	11.17	11.76	10.28	11.69	12.55	11.53

*Difference necessary for significance at 5% level: 2.17.

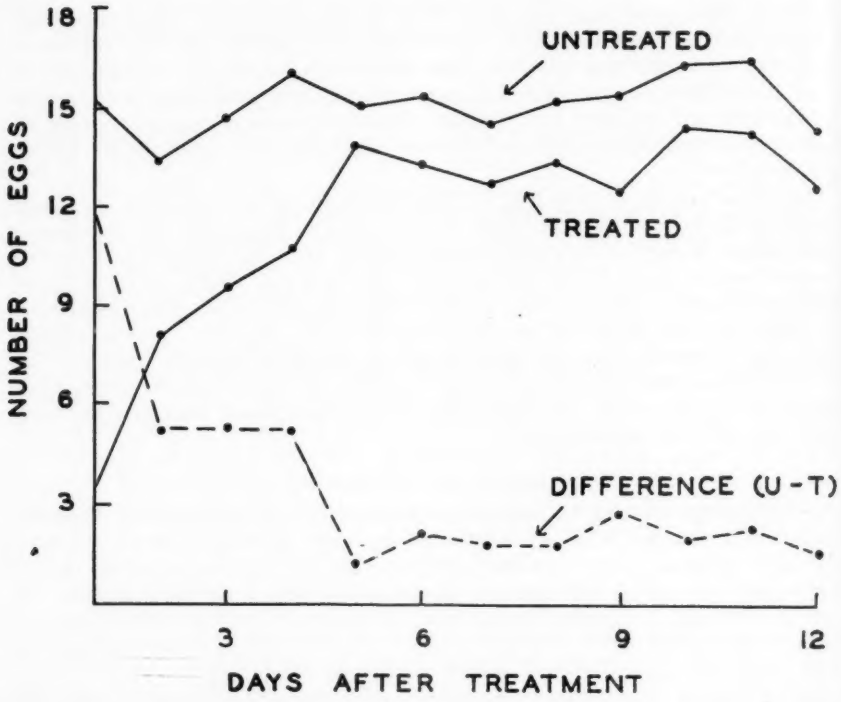

Fig. 1. Mean daily rate of oviposition of *T. confusum* exposed to 5 per cent *p-p'*-DDT residue for 1 hour at 32°C.

the difference between any two ordinates on the broken line (U-T) on the graph must be at least 3.3 to denote significance at the 5 per cent level. During the first four days after exposure, treated beetles laid significantly fewer eggs than untreated ones. The oviposition rate gradually increased from the first until the fifth day, after which it levelled off at a rate slightly but significantly lower than that of the untreated group.

This study showed that one effect of sublethal contact of females of *T. confusum* with residual deposits of DDT is reduced oviposition, especially in individuals that survive contact with heavy concentrations of the insecticide.

In practice, the effectiveness of an insecticide used to control insect infestations is based on insect mortality. This study showed that further effects occur in the reduction of oviposition of flour beetles surviving exposure. Presumably this effect has practical significance in retarding population increases in flour mills and other food storage establishments. Thus control of flour beetles with DDT may be greater than that shown by mortality data alone.

Summary

The rate of oviposition of *T. confusum* surviving exposure to 10 or 25 per cent residues of *p-p'*—DDT was significantly reduced during a period of observation from the seventh to the twenty-sixth day after exposure; this effect was not observed in females surviving exposure to one, three, or five per cent residues.

Females surviving exposure to 5 per cent DDT laid significantly fewer eggs than unexposed females during the four days following exposure, the fewest being laid on the first day.

Acknowledgment

Thanks are due to Dr. J. W. Arnold of the Ottawa laboratory for reading the manuscript and offering constructive suggestions.

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The Genus *Epipagis* Hubner, *nec* Hampson, in North America (Lepidoptera: Pyralidae)[1]

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Hübner ([1824-25] p. 357) defined the genus *Epipagis*, citing three species. Hampson (1918: 277) chose *fenestralis* Hübner as type, and sank *Sameodes* Snellen to *Epipagis*. The arrangement of the British Museum Pyralidae shows that Hampson thought *fenestralis* Hübner was the same as *phyllisalis* Walker; but so far as I know this synonymy was never published. Actually, Hübner's figure of *fenestralis* represents a female of the genus usually known as *Stenophyes* Lederer, wrongly synonymized by Hampson (1899) with *Crocidophora* Lederer. The size and coloration suggest that the species Hübner figured is the common North American one universally called *huronalis* Guenée.

Epipagis, a name in current, though erroneous, use, must replace *Stenophyes* Guenée. However, so far as I know, no author since Hübner has used the name *fenestralis* in print for a recognizable species. Under the Copenhagen decisions on zoological nomenclature (Hemming, 1953, para. 28) *fenestralis* Hübner probably should not replace *huronalis* Guenée, although it would do so under the law of priority.

The name *Sameodes* should be applied to *cancellalis* Zeller and to species put in the same genus. *Sameodes* in the sense of Hampson is extremely heterogeneous, but I will not try at this time to separate the components.

So far as I know there are three species of *Epipagis* in North America. They can be separated by the following key:—

1. Hind wing with two transverse lines on the disc 2
   Hind wing with traces of one transverse line on the disc, preceded only by scattered dots ..... Species No. 1
2. Proximal line of hind wing strong, continuous to near anal margin ..... Species No. 3
   Proximal line of hind wing weak, distinctly broken behind cell ..... Species No. 2

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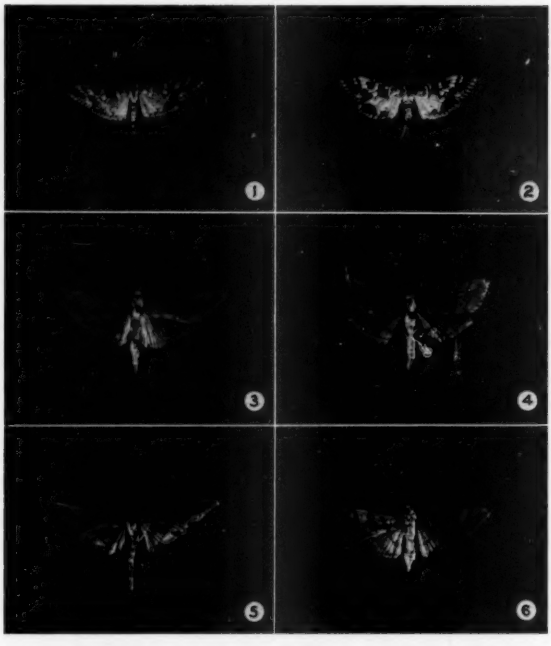

1. *E. forsythae.* Paratype, ♂. Florida City, Fla.; June 11, 1936; M. E. Forsyth. C.N.C.
2. *E. forsythae.* Allotype, ♀. Florida City, Fla.; May 9, 1938; M. E. Forsyth. C.N.C.
3. *E. huronalis.* ♂. Hope, Ark.; Sept. 16-19–; L. Knobel. C.N.C.
4. *E. huronalis.* ♀. Hope, Ark.; May 26, 1924; L. Knobel. C.N.C.
5. *E. disparilis.* ♂. Madera Canyon, Sta. Rita Mts., Ariz.; July 23, 1947; R. L. Ford. Coll. R. L. Ford.
6. *E. disparilis.* ♀. Huachuca Mts., Ariz.; Sept. 22, 1903; Oslar. British Museum (Natural History).

1. *Epipagis forsythae*, new species

Figs. 1, 2.

Male:—Head with mixed brown and white scaling; palpus brown above, white beneath. Thorax white, suffused with brown anteriorly above. Fore and mid legs brown anteriorly, white posteriorly; hind leg mostly white. Abdomen white, with irregular brown patches, especially mid-dorsally and on the posterior half of the venter. Fore wing above narrow and sharp-tipped, but not so strikingly so as in *huronalis;* ground-colour white, markings dark brown; sub-basal spot semicircular, fused with the dark brown costal area; antemedial line irregular, its general course perpendicular to costa; orbicular and claviform spots square, fused, reniform trapeziodal, all three solidly dark brown; postmedial line thick, regular, very weakly bent distad behind M_2, offset basad in front of Cu_2, crossed in this region by an oblique tornal patch; marginal patch extending from apex to M_3, where it peters out rather suddenly; terminal line black; fringe white with dark brown wedges opposite veins; veins brown-scaled, especially on disc. Hind wing white; a dark wedge on costa near base; a brown dot at lower angle of cell, a second about half-way along Cu_2, a third, indistinct one in the anal area; tornal and marginal patches as on fore wing, but less sharply defined, a trace of postmedial line extending forward from tornal patch; terminal line and

fringe as on fore wing. Markings of upper side repeated beneath, but less distinctly.

Male genitalia: tegumen and vinculum slender; uncus narrow, triangular, apex armed with apically directed spines; valve broad, thin, rounded apically; costa of valve narrowly tubular; clasper a ventrally directed spine near base of valve; juxta of moderate size, ovate; aedoeagus broadening posteriorly, with a heavy sclerotized strap in the left wall; a pair of trifid cornuti, each with a long, sharp postero-ventro-mesal process, a short, sharp postero-dorso-mesal process, and a short, blunt postero-exterior process.

Female genitalia: ovipositor lobes rather slender, bearing about four irregular rows of fine setae; apophyses slender; ostium without special features; ductus dilated dorsally just before ostium, and with a sclerotized collar just before the dilation; an accessory duct entering a dilation of the ductus just behind the bursa; bursa finely spiculate; signum a longitudinal groove, flanked on each side by about three rows of about 25 rather heavy, outwardly directed, closely apposed spines.

Holotype, ♂: Florida City, Fla.; May 18, 1938; Mrs. L. E. Forsyth. Allotype, ♀: same locality and collector; May 9, 1938. Paratypes: 1 ♂: same locality and collector; June 11, 1936. 1 ♂: Royal Palm State Park, Fla.; April 12-18, 1923; A.M.N.H. F.4672-S.

The holotype, allotype, and the Florida City paratype are No. 6165 in the Canadian National Collection of Insects; the other paratype is in the American Museum of Natural History.

This species is easily distinguished from *E. huronalis* by the darker and more strongly contrasting markings and by the reduced transverse lines of the hind wing. As typical specimens of *E. huronalis* were taken at Florida City during the same month as the holotype and allotype of *E. forsythae*, *E. forsythae* cannot be a seasonal or geographic variant of *E. huronalis*.

2. *Epipagis huronalis* (Guenée), new combination

Figs. 3, 4.

Pyralis Fenestralis Hübner, 1796, Pl. 9, Fig. 60.
Epipagis Fenestralis, Hübner, 1824-25, p. 358.
Samea huronalis Guenée, 1854: 198.
Phalangiodes serinalis Walker, 1859: 468.
Crocidophora huronalis, Hampson, 1899: 194 (in part).
Stenophyes huronalis, Fernald, 1902: 381.

The name *fenestralis* is older than *huronalis*, but as its use would apparently violate the principle of conservation, I retain the familiar name *huronalis*. Dyar (1910: 272) correctly pointed out that *Samea zinghalis* Walker (1859: 355), which Hampson sank as a synonym of *huronalis*, is really a distinct species; *zinghalis* does not occur in North America and the name should be deleted from the North American list.

Epipagis huronalis is the most common species of the genus in the United States. The distinctly fulvous tone of the dark markings of the forewing is distinctive; the hind wing is more fully marked than that of *forsythae*, less so than that of *disparilis*.

Genitalia of both sexes closely similar to those of *E. forsythae*. Cornuti of male with processes slightly shorter and thicker; signum of female a little longer, bursa more heavily spiculate, and collar extending into the dilated portion of the ductus on each side; signum on each side with three or four rows of about 40 spines each.

I have examined a considerable series of specimens from the following states:

Florida, Georgia, South Carolina, North Carolina, Tennessee, Arkansas, Louisiana and Texas. The type locality of *huronalis* is given as Canada, that of *fenestralis* as Europe. Presumably both are erroneous.

3. *Epipagis disparilis* (Dyar), new combination

Figs. 5, 6.

Stenophyes disparilis Dyar, 1910: 271.

I have not seen the type, but Dyar's description cannot be misinterpreted. This species can be distinguished in both sexes from all others of the genus by the heavy and continuous antemedial line of the hind wing. This is the largest species of the genus, small specimens being as large as large specimens of *E. huronalis*. The markings are darker than in *E. huronalis*, but lighter than in *E. forsythae*. The male has the apex of the fore wing exceptionally prolonged and acute. The fore wing in both sexes has the reniform spot joined to the tornal patch by a definite oblique bar, which appears to form the transverse segment of the postmedial line.

Male genitalia with processes of cornuti short and stout. Female genitalia similar to those of *E. huronalis*, but with bursa more heavily spiculate, and with groove of signum flanked by two or three rows of over 50 spines.

This species was described from Mexico, and has not been recorded from the United States. Some time ago, Mr. Robert L. Ford, South Gate, Calif., loaned me a male that he collected at Madera Canyon, Santa Rita Mountains, Ariz., on July 23, 1947. I have since seen four additional Arizona specimens: a male in the American Museum of Natural History from El Mirador Ranch, 4 miles west of Sasabe, Baboquivari Mts., Sept. 1950; and in the British Museum (Natural History) a male, Southern Arizona, July 15-30 (Poling), and two females, Huachuca Mts., Sept., 1903 (Oslar). The Arizona specimens agree well with specimens from Guadalajara and other localities in southern Mexico.

Acknowledgments

I am indebted to the following colleagues, who have helped me by loaning material and in other ways: Mr. Harry K. Clench, Carnegie Museum, Pittsburgh, Pa.; Mr. Robert L. Ford, South Gate, Calif.; Mr. C. P. Kimball, Barnstable, Mass., and Sarasota, Fla.; Professor A. K. Klots, City College of New York; Mr. E. L. Martin, British Museum (Natural History), London, England; and Dr. F. H. Rindge, American Museum of Natural History, New York, N.Y.

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Descriptions and Habits of Cecidomyiidae (Diptera) from White Spruce Cones[1]

By HOWARD A. TRIPP

Introduction

Taxonomically, the Cecidomyiidae (Gall Midges) are a difficult group. Many species have been described using colour of freshly killed specimens as the principal criterion for identification (Felt, 1907a). As dead specimens seldom retain their original colour, subsequent determinations based on this characteristic are almost impossible. Morphological characteristics which separate the genera are fairly distinct and therefore acceptable but those used to separate the species, namely, the number and shape of the antennal segments (Barnes, 1932), were found to be quite variable in the species studied. Species are more easily identified if, in addition to their morphology, something is known of their biology. In this paper, descriptions and notes on the biology of five gall midges from white spruce cones are given. In addition, the literature on all species from white spruce is reviewed.

Review of the Literature

In North America, four species of Cecidomyiidae have been described from spruce and presumably all from white spruce, *Picea glauca* (Moench) Voss., (Barnes, 1951, p. 80). Only one, *Dasyneura canadensis* Felt, the fir or spruce seed midge, has been reared from the cones. The other three species are the spruce bud midge, *Rhabdophaga swainei* Felt, the spruce gall midge, *Phytophaga* (= *Mayetiola*) *piceae* Felt, and *Phytophaga* (= *Mayetiola*) *tsugae* Felt which is also commonly called the spruce gall midge.

Dasyneura canadensis was first described (Felt, 1907b, p. 157) from specimens supposedly reared from seeds of white spruce but the scientific name of the host was given as "*Abies alba*". This apparent error led to considerable confusion in subsequent publications. In his redescription, Felt (1915) gives white spruce as the host tree (p. 162) but the same author also refers to the species as being "bred from seeds of *Abies* (spruce)" (1908, p. 336) and "*Abies* (fir)" (1917, p. 18) (1940, p. 45). Nevertheless, his illustration (1940, p. 45) depicts a cone resembling one from white spruce rather than fir.

The common name, "fir or spruce seed midge", has also led to the statements that *D. canadensis* causes considerable loss of white spruce seed (Felt, 1914, p. 76) and (Stewart, 1943). The present study has shown, however, that *D. canadensis* does not attack the seed, the injury being caused by two other species of cecidomyiids which are described in this paper. Other insects causing damage to the seed are the spruce seedworm, *Laspeyresia youngana* (Kft.), an olethreutid (Tripp, 1954b) and *Pegohylemyia anthracina* Czerny, an anthomyid (Tripp, 1954a).

Rhabdophaga swainei, the spruce bud midge, was described (Felt, 1914, pp. 77-78) from specimens reared by J. M. Swaine, Ottawa, Canada, from spruce buds but in one instance (Felt, 1917, p. 18) the host tree was listed as fir. However, a recent account by Clark (1952) lists only *Picea* as hosts, namely, white spruce, *P. glauca*, red spruce, *P. rubens* Sarg., Norway spruce, *P. abies* (L.) Karst., and Colorado blue spruce, *P. pungens* Engelm. The insect infests the buds, usually the terminal ones, causing bud hypertrophy. Other buds develop which

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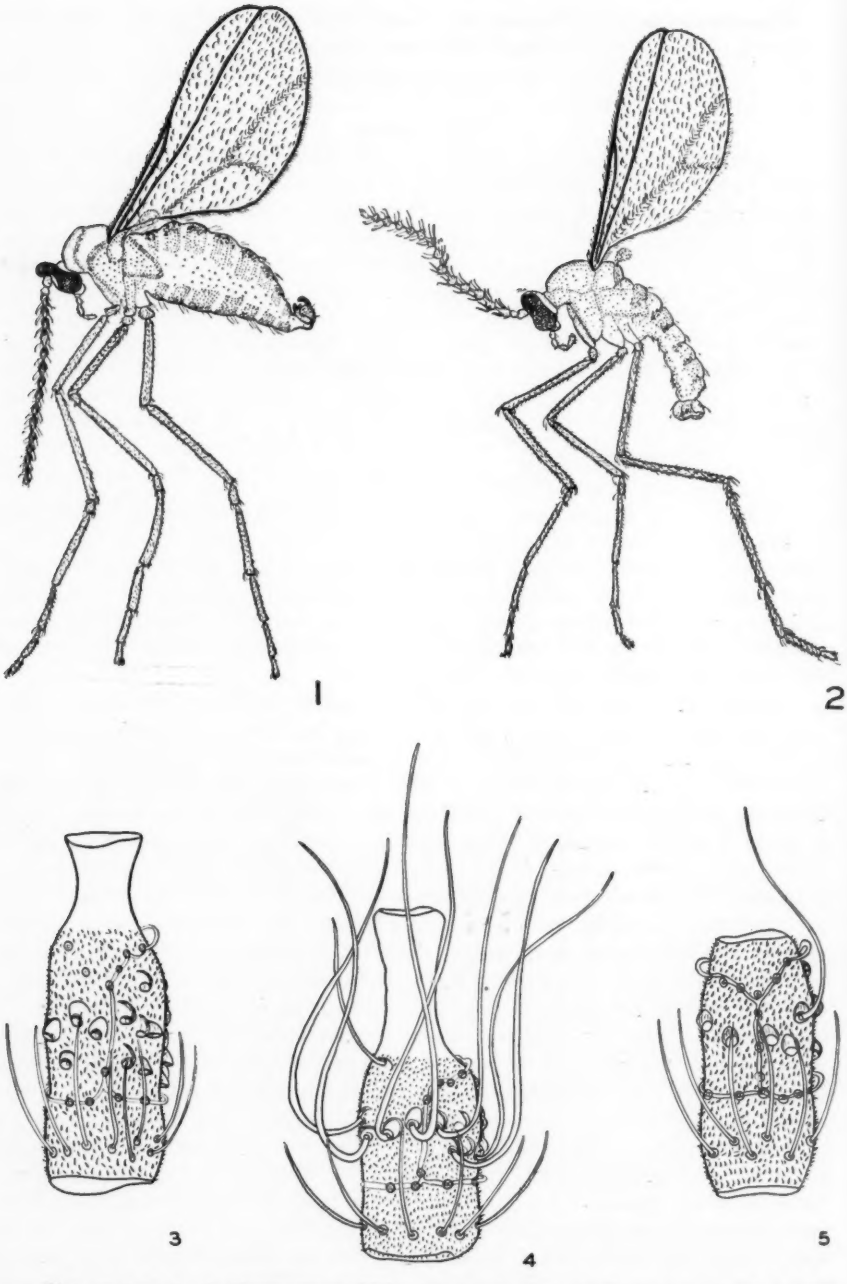


Figs. to 1 to 5. 1. *Dasyneura rachiphaga* n. sp. (male). 2. *Dasyneura canadensis* Felt (male). 3. Fifth antennal segment of *D. rachiphaga* (male). 4. Fifth antennal segment of *D. canadensis* (male). 5. Fifth antennal segment of *D. rachiphaga* (female) (similar in *D. canadensis*).

in turn may be infested giving the tree a bushy effect. The type of injury is well illustrated in Clark's paper.

Phytophaga piceae, the spruce gall midge, was described (Felt, 1926) from specimens reared by Swaine from the twigs and needle-bases of white spruce. Recently, Smith (1952) published a brief description of the insect and an account of its habits and damage. It infests the bases of the needles giving the twig a swollen and warty appearance. The current growth is killed, a severe infestation making the tree very unsightly. Indeed, small white spruces near Stittsville, Ontario were killed in 1952, apparently by the attacks of this insect. The nature of the injury may be readily recognized by referring to the illustrations in Smith's paper.

Phytophaga tsugae, also commonly called the spruce gall midge, was described by Felt (1907a, p. 27) from a single male taken on hemlock. He placed it in the genus *Oligotrophus* Latr. He later (1916, p. 207) redescribed the male and described the female from specimens reared from spruce bud galls by Swaine. In later references (Felt, 1917, p. 18) (Felt, 1940, p. 45) the species is called the spruce gall midge but with fir (*Abies*) given as the host tree. To add to the confusion, the type of injury attributed to this species (Felt, 1917, p. 18) is typical of that of *P. piceae*. A comparison of the types of these species might show them to be identical.

***Dasyneura canadensis* Felt**

Figs. 2, 4, 12, 16, 19, 20, 24, 27.

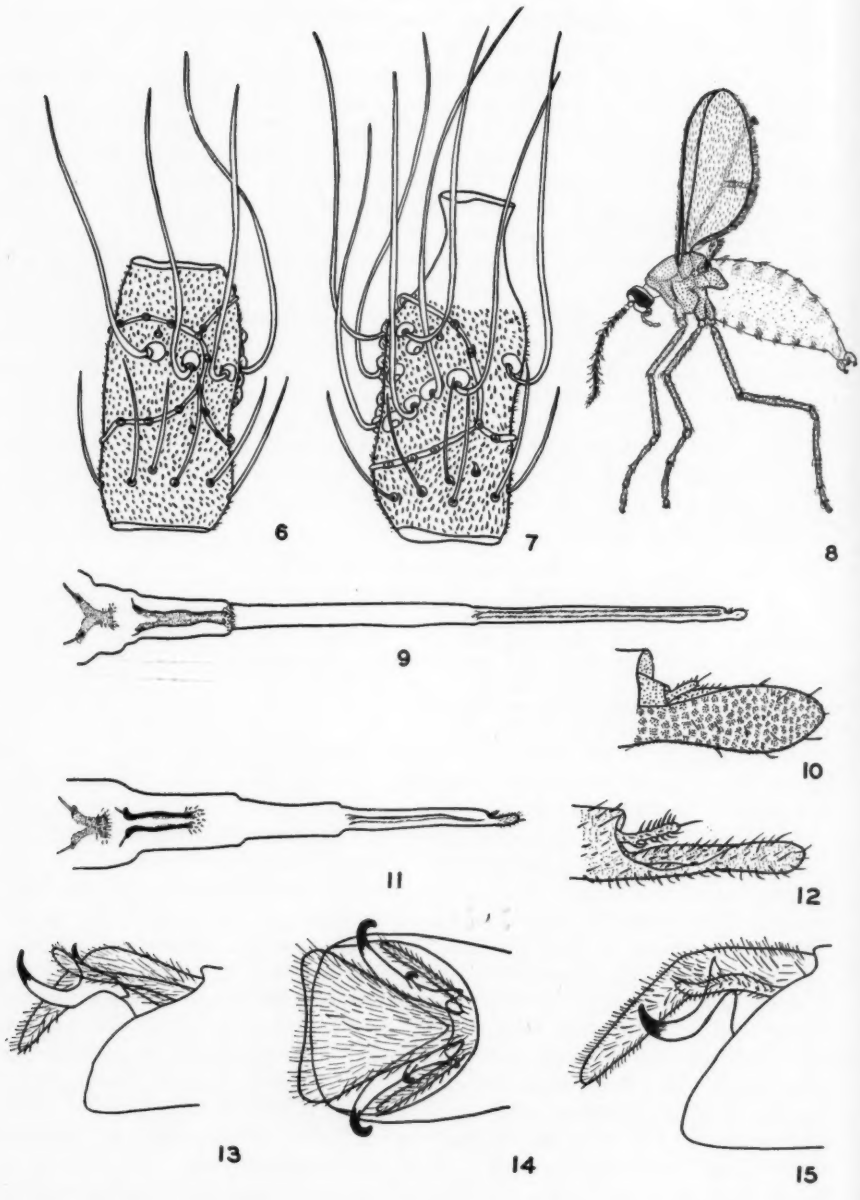
1907, Felt. E. P., N.Y. State Mus. Bull. 110: 157.
1908, Felt. E. P., N.Y. State Mus. Bull. 124: 347, 350.
1915, Felt. E. P., N.Y. State Mus. Bull. 175: 124, 129, 162.
1917, Felt. E. P., N.Y. State Mus. Bull. 200: 18, 19.
1940, Felt. E. P., Plant Galls and Gall Makers: 45.
1943, Stewart, K. E., Can. Ins. Pest Rev. 21: 51.
1951, Barnes, H. F., Gall Midges of Economic Importance 5: 80, 81.

Egg:—(Fig. 16). Oblong, 0.30 mm. long by 0.12 mm. wide. Whitish and translucent. Chorion smooth.

Larva:—Length, when full-grown, 3.00 mm. Thirteen segments, segmentation distinct (Fig. 20). Colour, when fresh, orange; anterior one-fourth and a pair of longitudinal dorsal and ventral narrow stripes dark orange; remainder light orange. Nine pairs of dome-shaped spiracles, one pair on each of the lateral margins of segment 2 (Fig. 19) and segments 5 to 12. Integument coarsely shagreened (Fig. 19), except around each spiracle where it is finely shagreened. A single transverse row of widely spaced, minute spines medially located on segments 2 to 13 inclusive; these spines somewhat larger and in a more regular row on the anterior segments (Fig. 19). Head (Fig. 19) faintly sclerotized and normally retracted into the thorax, rounded with a pair of lateral processes and a pair of median processes extending posteriorly from the oral aperture. Oral aperture sucker-like with several tiny rasp-like teeth surrounding the opening. Antenna small, inconspicuous with indeterminate segmentation.

Pupa:—About 2.50 mm. long. Antennal horn (Fig. 24) stout and rounded, weakly bidentate, teeth about equal in size.

Adult:—*Male* (Fig. 2). Body length approximately 2.00 mm. Antenna about 1.50 mm., normally 17 segments; stem of fifth segment (Fig. 4) nearly as long as basal enlargement; second to last segment sessile or nearly so; basal enlargement of segments 3 to 15 more or less globose, covered with numerous small setae and two whorls of long setae; basal whorl about half the length of basal enlargement;



Figs. 6 to 15. 6. Fifth antennal segment of *Phytophaga carpophaga* n. sp. (female). 7. Fifth antennal segment of *P. carpophaga* (male). 8. *P. carpophaga* (male). 9. Ovipositor of *P. carpophaga*. 10. Tip of ovipositor of *P. carpophaga*. 11. Ovipositor of *Dasyneura rachipaga* (that of *D. canadensis* similar). 12. Tip of ovipositor of *D. canadensis* (that of *D. rachiphaga* similar). 13. Tarsal claw, empodium and pulvillus of *P. carpophaga*. 14. Tarsal claws, empodium and pulvilli of *D. rachiphaga* (similar in *D. canadensis*). 15. Tarsal claw, empodium and pulvillus of *D. rachiphaga* (similar in *D. canadensis*).

anterior whorl about as long or longer than the entire segment. Circumfila very slightly raised from the segments, each circumfilum (Fig. 4) encircling its segment near the base and with a loop over one anterior shoulder of the basal enlargement, rejoining the basal ring on the opposite side. Palpus (Fig. 23) 4-segmented; length about 0.25 mm., basal segment smallest, subrectangular; second a little longer, oval; third longer than the second but not as wide; fourth a little longer than the third. Tarsal claw (Fig. 14, 15) with hook-like basal tooth. Pulvilli slender, shorter than the claws and partially obscuring the basal teeth. Empodium (pulvilli of Felt, 1915, p. 162) spatulate, longer than the claws. Front tarsus about 1.10 mm. long, about 1.75 the length of the tibia. Genitalia (Fig. 27) with basistyle stout, about twice as long as wide; dististyle rather slender, about three times as long as wide, with a slight constriction on the outer surface near the apex; dorsal plate broad, deeply emarginate apically; ventral plate narrower, tapering slightly to the apex, only moderately emarginate at apex.

Female. Length excluding ovipositor and antennae 2.00 mm. Antenna about 0.80 mm., usually with 15 segments but sometimes varying from 13 to 16; all segments sessile, or nearly so, with terminal two usually fused; fifth (Fig. 5) with setae similar to those of male but the anterior whorl usually shorter. Circumfila similar to those of male but with a circumfilum (Fig. 5) looping over each anterior shoulder of segment. Ovipositor (Fig. 11) longer than abdomen, about 2.20 mm. when fully extended; terminal lobes (Fig. 12) long and slender. Other characters as in the male.

Type locality, Ottawa, Canada. Type (a1428) in New York State Museum collection.

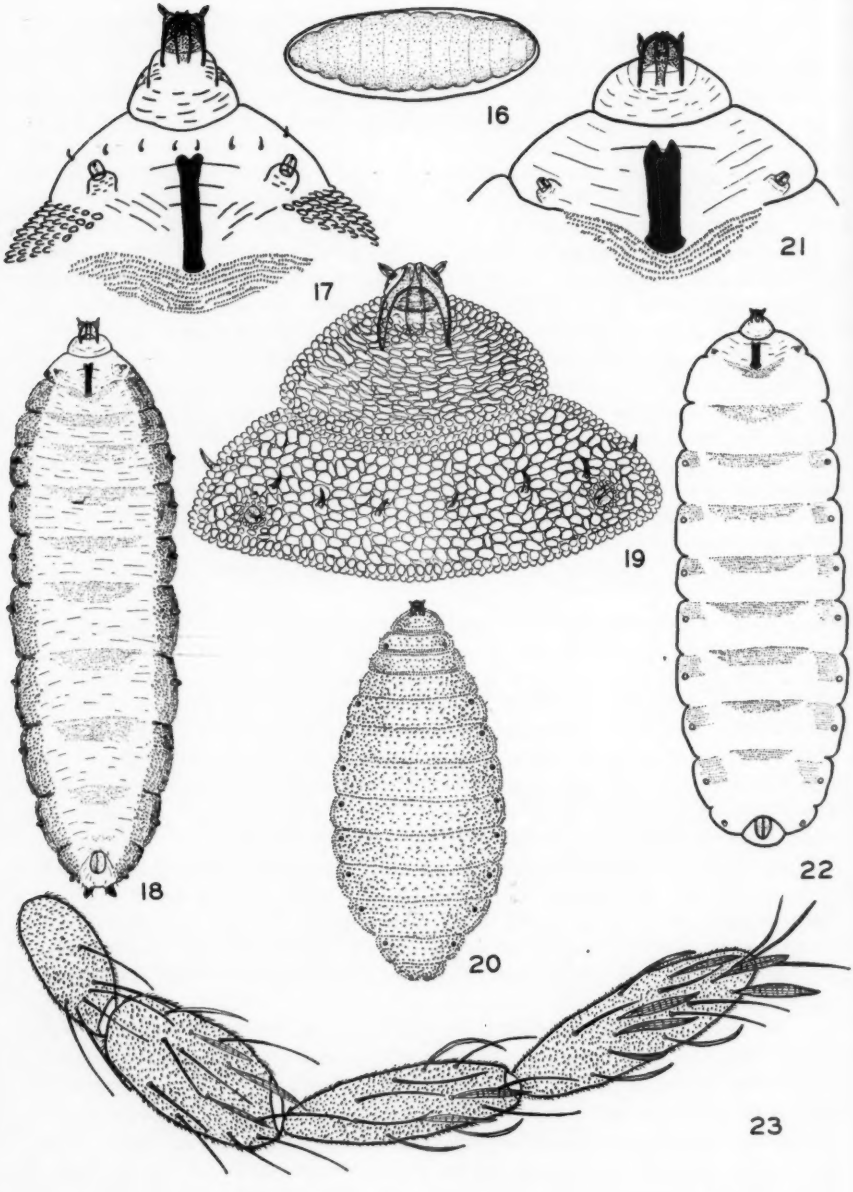
Biology:—*D. canadensis* attacks the scales of white spruce cones. The larvae form small galls in the scale tissue and when abundant give the cone a warty appearance. The production of apparently sound seed, however, is not appreciably affected. Occasionally, a gall is formed adjacent to a developing ovule and in such cases the seed is destroyed but the insect is primarily scale-inhabiting.

It was found to be the most prevalent cecidomyiid in white spruce cones. Even when cones were very abundant and cecidomyiids relatively scarce, about 90 per cent of the cones were infested with an average of eight galls per cone. When cones were scarce, close to 100 per cent were infested.

The eggs are deposited in lots of two to three on the scales when the cones are open for the acceptance of pollen which usually occurs about mid-May. The stickiness of the scales at this time holds the eggs firmly in place. It is not unusual, when cones are scarce, to find 15 to 20 eggs in a cluster resulting from the oviposition by different females. In 1951, a sample of 10 cones averaged 137 eggs per cone.

Although nearly all eggs hatch, only a few larvae survive. This is probably a direct result of overcrowding. In 1950, two weeks after hatching, an average of 16 larvae per cone had started galls but by the end of June only 8 larvae per cone were found to be successfully established.

Newly-hatched larvae are inconspicuous and often difficult to locate. They burrow through the seed wings and in a few weeks small swellings appear on the inner surface of the scales. Each swelling indicates the presence of a single cecidomyiid larva. As the larva increases in size, the gall pocket is enlarged and the surrounding tissue becomes hard. By July, the gall is plainly visible from both sides of the scale. It is oblong in shape with its long axis directed along the long axis of the scale. About mid-July, the larva makes a small exit hole at the upper end of the gall. After sealing this opening with silk, it spins a tightly



Figs. 16 to 23. 16. Egg of *Dasyneura canadensis* (eggs of *D. rachiphaga* and *P. carpophaga* similar). 17. Anterior segments of unidentified larva (Species B). 18. Unidentified larva (species B). 19. Anterior segments of larva of *D. canadensis*. 20. Larva of *D. canadensis* (larvae of *D. rachiphaga* and *P. carpophaga* similar). 21. Anterior segments of unidentified larva (Species A). 22. Unidentified larva (Species A). 23. Palpus of *D. rachiphaga* (that of *D. canadensis* similar).

woven cocoon and passes the winter in this condition. Pupation occurs in late April or early May and about mid-May the adult emerges through the exit hole made the previous autumn. The pupal skin generally remains in the cocoon but is sometimes found protruding from the exit hole.

In common with most other white spruce cone insects, *D. canadensis* was observed to undergo diapause. Several larvae from 1950 cones failed to pupate until 1952.

Dasyneura rachiphaga n. sp.

Figs. 1, 3, 5, 11, 14, 15, 23, 25, 30.

Egg:—similar to that described for *D. canadensis* (Fig. 16).

Larva:—Length, when full-grown, 3.00 mm. Colour, when fresh, yellowish-orange. Otherwise similar to *D. canadensis* (Figs. 19, 20).

Pupa:—Nearly 3.00 mm. long. Antennal horn (Fig. 25) unidentate, pointed and strongly acute.

Adult:—*Male* (Fig. 1). Body length approximately 2.20 mm. Antenna about 1.50 mm., normally 17 segments, rarely 18; terminal two segments usually fused. Stem of fifth segment (Fig. 3) usually less than half as long as the basal enlargement. Basal enlargement of segments 3 to 15 more or less truncate. Front tarsus about 1.4 mm. long, about 1.75 the length of tibia. Other characters similar to *D. canadensis*.

Female. Length excluding ovipositor and antennae 2.20 mm. Antenna about 1.00 mm., 16 or 17 segments with terminal two usually fused. Other characters, except for size, as in *D. canadensis*.

Holotype:— ♂, Kemptville, Ontario, Canada, May, 1954 (Tripp). Number 6255, in the Canadian National Collection, Ottawa, Canada.

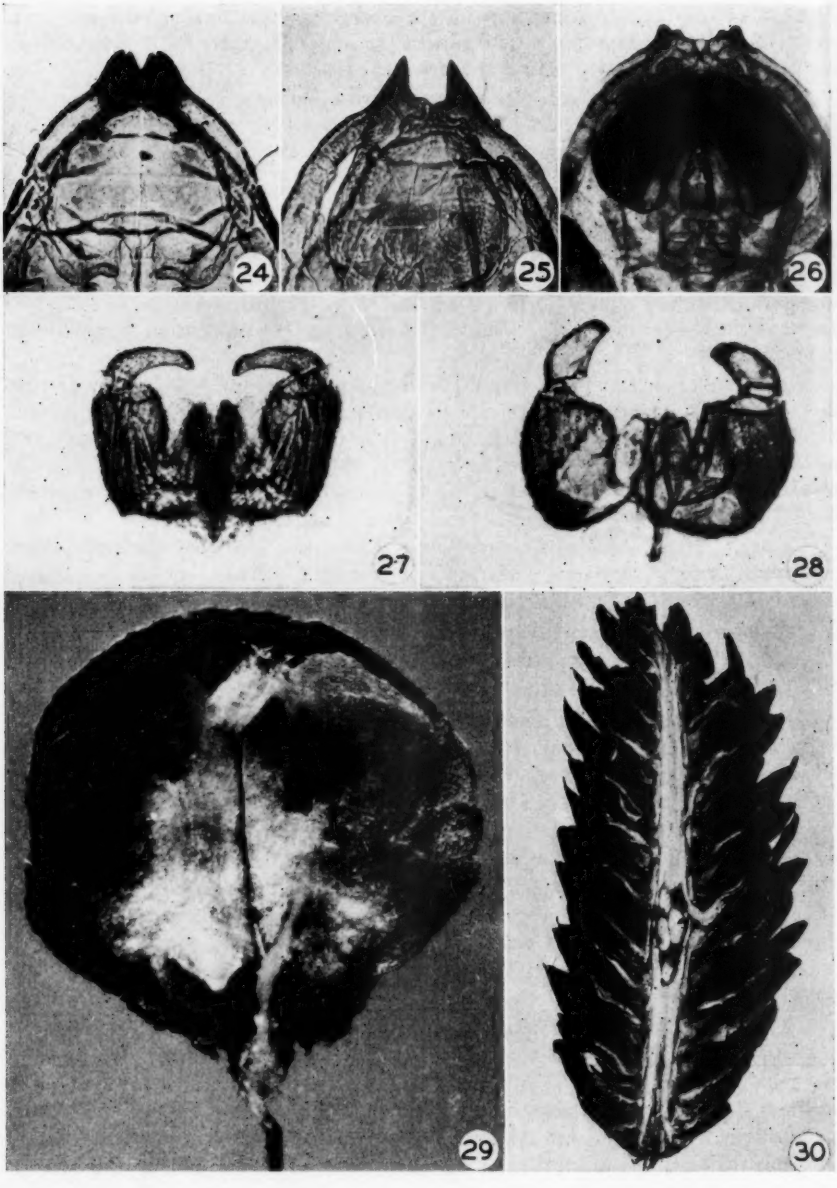
Allotype:— ♀, same data as holotype.

Paratypes:—4 ♂, 4 ♀, same data as holotype. 1 pupa, Kemptville, Ontario, Canada, May 7, 1953 (Tripp); 1 pupa, Stittsville, Ontario, Canada, May 1, 1952 (Tripp) and 2 larvae, Quyon, P.Q., Canada, Sept. 28, 1950 (Tripp)—all in the Canadian National Collection, Ottawa, Canada. 1 ♂, 1 ♀, same data as holotype, and 1 pupa, Stittsville, Ontario, Canada, May 1, 1952 (Tripp) in the United States National Museum, Washington, D.C.

Biology:—The larvae make small gall-pockets in the rachis of white spruce cones (Fig. 30). As they do not come in contact with the seeds they cause them no direct injury. However, in some cones the rachis may be almost completely filled and possibly some injury may result to the seeds from the destruction of the conductive tissue.

The life cycle of *D. rachiphaga* is similar to that of *D. canadensis* but there is a difference in habits. Although the eggs are structurally similar to those of *D. canadensis* it is reasonable to assume that eggs deposited at the extreme bases of the scales, near, or on the rachis, are those of *D. rachiphaga*. On hatching, each larva makes its way into the tissue at the extreme base of a scale where a small cavity is formed. As it approaches maturity it makes a small hole at the base of the scale just beneath the corresponding bract. A thin layer of silk covers the hole through which the adult eventually emerges. During the latter part of July, the larva makes a silk-lined passage into the rachis. Here it constructs a cocoon by simply sealing itself off in the blind end of the silken tube. Such cocoons are readily identified even when removed from their habitat.

The winter is passed in the larval stage and pupation occurs in April. Adults



Figs. 24 to 30. 24. Pupal antennal horns of *Dasyneura canadensis*. 25. Pupal antennal horns of *D. rachiphaga*. 26. Pupal antennal horns of *Phytophaga carpophaga*. 27. Male genitalia of *D. canadensis*. 28. Male genitalia of *P. carpophaga*. 29. Galled seed and pupal skin of *P. carpophaga*. 30. Cocoons of *D. rachiphaga* in rachis of cone.

emerge in mid-May, slightly in advance of *D. canadensis*, leaving the pupal case in the cavity or partly protruding from the exit hole.

Phytophaga carpophaga n. sp.

Figs. 6, 7, 8, 9, 10, 13, 26, 28, 29.

Egg:—Similar to that described for *D. canadensis* (Fig. 30).

Larva:—Colour pink. Otherwise similar to *D. canadensis* (Figs. 11, 12).

Pupa:—About 3.00 mm. Antennal horn (Fig. 3) short, weakly bidentate, the inner tooth shorter than the outer, the latter minutely notched.

Adult:—*Male* (Fig. 8). Body length 2.40 mm. Antenna about 1.30 mm. with 17 segments, terminal two usually fused; fifth (Fig. 7) with stem about one-third as long as the basal enlargement; basal enlargement more or less truncate. Circumfila similar to those of *D. canadensis*. Tarsal claws (Fig. 13) simple, strongly curved. Pulvilli slender, shorter than the claws. Empodium spatulate and longer than the claws. Palpus 4-segmented; length about 0.25 mm.; basal segment smallest, rectangular; second a little longer, oval; third and fourth about equal in length and longer than the second. Front tarsus about 1.00 mm. long and about 1.33 the length of the tibia. Genitalia (Fig. 28) with basistyle about twice as long as wide; dististyle wider at base, about twice as long as its basal width. Dorsal plate broad, deeply emarginate apically; ventral plate narrower, sides straight or slightly tapered at base, moderately emarginate at apex.

Female. Length excluding ovipositor and antennae 2.30 mm. Antenna about 1.00 mm. long with 16 segments, terminal two usually fused; fifth (Fig. 6) similar to that of *D. canadensis* but shorter, making is appear stouter. Ovipositor (Fig. 9) longer than the entire body, when fully extended about 3.30 mm.; terminal lobes (Fig. 10) short and rather bulbous. Other characters as in the male.

Holotype:—♂, Dunrobin, Ontario, Canada, May 7, 1953 (Tripp). Number 6256, in Canadian National Collection, Ottawa, Canada.

Allotype:—♀, same data as holotype.

Paratypes:—2 ♂, same data as holotype; 2 ♂, 1 ♀, Huntley, Ontario, Canada, May 7, 1953 (Tripp); 3 pupae (1 slide), Dunrobin, Ontario, Canada, May 6, 1953 (Tripp); 3 larvae, Stittsville, Ontario, Canada, July 15, 1950 (Tripp)—all in the Canadian National Collection, Ottawa, Canada. 1 ♂, Huntley, Ontario, Canada, May 7, 1953 (Tripp) and 1 ♀, 2 pupae (1 slide), same data as holotype, in the United States National Museum, Washington, D.C.

Biology:—This species attacks the seeds of white spruce cones. Its life-cycle is similar to that of the *Dasyneura* species in the cone. Eggs are deposited in late May, larvae spin cocoons in July, pupate in April, and adults emerge in early May. Some larvae remain in diapause over the second summer.

Although the eggs cannot be distinguished morphologically from those of *D. canadensis* or *D. rachiphaga*, they may be identified by their position near the ovule micropyles. Upon hatching the larvae work their way through the micropyles into the ovules. In a few weeks these ovules exhibit an abnormal swelling and are pale green while normal ovules are streaked with red at this stage. Gradually, as the larvae mature, the infested ovules become shiny brown, brittle, and misshapen (Fig. 29). As they are somewhat larger than normal seeds, they are held more firmly by the scale and thus do not drop to the ground during normal seedfall. The cocoons of this species, when removed from the seed, may be distinguished from those of the other species in the cone by their larger size.

Other White Spruce Cone Cecidomyiids

Two other species of Cecidomyiidae attack white spruce cones but larvae of these were present in comparatively few cones. Despite attempts to rear them, only the larval stages were obtained. Since there is a strong possibility that their adult stages may be described, they are designated simply as Species A and Species B.

Species A

Figs. 21, 22.

Larva:—About 3.50 mm. long. Thirteen segments; segmentation distinct. Nine pairs of dome shaped spiracles located on the lateral margins of segments 2 and 5 to 12. Colour, when fresh, orange. Integument smooth except for several transverse lines of very minute spines at the anterior of each segment except the first two and the last, and a patch of similar spines just anterior to each spiracle except the first. Head similar to that of *D. canadensis* except narrower and more heavily sclerotized. Breastplate present, about four times as long as wide; teeth acute, shaft broad and rounded at base.

Biology:—Larvae infest the seeds. Infested seeds were difficult to detect as they exhibited no apparent external evidence of attack. Dissection of each seed in the cone was necessary and in the process several larvae were injured. However, about a dozen apparently healthy larvae were obtained and held in rearing tubes for over a year. They died without pupating or spinning cocoons. It is quite possible that they require two years to complete their cycle.

Species B

Figs. 17, 18.

Larva:—About 4.00 mm. long. Head and spiracles similar to those of Species A. Colour, when fresh, very deep orange to red. Several transverse rows of very minute spines at the anterior of each segment except the first two. Lateral edges with numerous minute but conspicuous papilli. A pair of prominent sclerotized processes at the posterior end. Breastplate present, about six times as long as wide; teeth rounded; shaft broad and rounded at base.

Biology:—Larvae were found feeding apparently as scavengers between the seed wings and scales of the cone. They left the cones in the fall, presumably to pupate in the duff beneath the trees.

Summary

The literature on the gall midges attacking white spruce is reviewed. Observations on the seasonal history, habits, and descriptions of all stages of *Dasyneura canadensis* Felt are given. Two new species, *Dasyneura rachiphaga* and *Phytophaga carpophaga*, are described with notes on their seasonal history and habits. Descriptions and notes on two unidentified cecidomyiid larvae found in the cones are also given. The principal differences between the species are summarized in the following key.

Larvae

1	Breastplate present	2
	Breastplate absent	3
2	Breastplate 4 times as long as wide; larva orange; in seed	Species A
	Breastplate 6 times as long as wide; larva deep orange to red; between scale and seed wing	Species B
3	Light and dark orange; in scale	*D. canadensis*
	Yellowish-orange; in rachis	*D. rachiphaga*
	Pink; in seed	*P. carpophaga*

Pupae

1	Antennal horns unidentate	*D. rachiphaga*
	Antennal horns bidentate	2
2	Teeth of horns equal in size	*D. canadensis*
	Inner tooth of each horn short	*P. carpophaga*

Adults

1	Tarsal claw simple	*P. carpophaga*
	Tarsal claw with hook-like tooth	2
2	Antennal segments sessile (females)	3
	Antennal segments stemmed (males)	4
3	Usually 15 antennal segments, rarely 16	*D. canadensis*
	16 or 17 antennal segments	*D. rachiphaga*
4	Fifth antennal segment with stem nearly as long as basal enlargement	*D. canadensis*
	Fifth antennal segment with stem about half as long as basal enlargement	*D. rachiphaga*

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Mortality Factors Acting in a Sequence

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In 1910 in a paper on the parasites of the Gypsy and Brown-tail moths, W. F. Fiske[1] calculated the mortality necessary to stabilize the gypsy moth population and stressed the importance of a sequence of parasites and predators attacking successive stages of the insect host, in the establishment and maintenance of satisfactory control. In 1912, in the bulletin entitled "The Importation into the United States of the Parasites of the Gypsy Moth and Brown-tail Moth",[2] L. O. Howard and W. F. Fiske studied the problem of a sequence of parasites much more fully. They then made the very important point that aggregate percentage of kill necessary for the control of an insect pest could not be secured by simply adding together the figures representing the kills resulting through attack by each of two or more species. It was going to be necessary, they said, to combine these several aggregates in a different manner. Thus a 50% parasitism of the eggs if it could possibly be secured, followed by another 50% parasitism of the caterpillars, could not by any possibility be considered as resulting in 100% parasitism or complete extinction but only in 50% parasitism added to 50% of what remained which amounted in effect to 25% of the whole. In this manner an aggregate of 75% only is secured. They said further that any specific amount of parasitism as 20% of the eggs, was neither more nor less, but exactly as effective as 20% parasitism of the caterpillars and pupae, in so far as its value in constructing the final aggregate was concerned. The principle they thus established, though it may seem obvious enough, had not apparently been previously recognized by workers on biological control and it is of the very greatest importance.

In 1928, in a paper published in Parasitology,[3] I was led to inquire why fluctuations in the percentage of parasitism of a certain stage of an insect may be quite considerable and yet there is no marked alteration in the density of the host and the damage it causes. In the course of this study I distinguished, as Howard and Fiske had done between the *apparent mortality* (that is to say, the mortality observed in a particular stage of the life-cycle, after the operation of preceding factors and before the operation of later factors) and the *real mortality:* the percentage mortality of the population which existed at the beginning of the life-cycle or, in other words, the *number of individuals* killed by all factors during the whole of the life-cycle. Using these formulae I showed that there may be fairly large fluctuations in the apparent mortality of a particular stage, without much alteration in the total mortality. However, I pointed out that controlling factors can be divided into two main classes, the *general* and the *individualized* factors. The class of general factors comprises those whose destructive capacity is independent of the numerical value of the host population; the class of individual factors comprises those whose destructive capacity depends in some way on the numerical value of the host population. The mortality resulting from the action of meteorological causes or from the intrinsic fragility of the organism in certain stages of development, is apparently about the same under given conditions whether the population is large or small. Thus, in rearing insects under laboratory conditions we find that whether the number handled is small or large, approximately the same portion of adults is secured. The proportion of eggs failing to hatch and the death rate in a given stage under given conditions, remain practically constant, whatever be the population handled. The parasites, on the contrary, are controlling factors of the second class. The

1Boston, Mass., Wright and Potter Printing Co., State Printers.
2U.S. Dept. Agr., Bur. Ent., Bull. 91.
3Vol. XX, No. 1, pp. 90-112.

number of hosts the female individual of a given species is capable of destroying is ordinarily determined by her reproductive capacity, which is a specific and constant character. Provided all the hosts are equally accessible, a parasite capable of depositing one hundred eggs could kill 10% of a population of one thousand hosts but only 1% of a population of ten thousand hosts. On the other hand, if all the hosts are not equally accessible the effective reproductive rate of the parasite may, under certain conditions, fall far below the potential reproductive rate.

Following a suggestion of H. S. Smith,[4] these two classes of factors are now commonly designated as *density-independent* and *density-dependent*. This terminology has the advantage of concentrating attention on an important characteristic of parasites and predators: their dependence on a supply of hosts for reproduction and the probability that the effective reproductive rate will rise when hosts are abundant and fall when hosts are scarce. Nevertheless, as I have already said, there is a certain maximum beyond which the effective reproductive rate cannot rise no matter how abundant the hosts. Furthermore, there are predators like birds, of which each family occupies a certain well circumscribed territory, in which it collects approximately the same amount of food material, in the selection of which it is not very specific. Such predators presumably endeavour to collect approximately the same amount of food material every season, so that if the host increases beyond a certain point, the *percentage* destruction falls, while if a particular host becomes scarce, no special effort will be made to find it but it will be replaced on the menu by a more abundant species. To take all these factors as density-dependent is therefore an ultra-simplication. It must be noticed also that if the parasites and predators are density-dependent this is because they are *individuals* with specific requirements. Density-dependence is a *secondary*, not a primary characteristic. Finally, variation in reproductive rate is not by any means altogether dependent on the density of the prey. It is affected by physical factors such as humidity and temperature, as well as by nutrition and the failure or inadequacy of fertilization. Too much concentration on host density may lead to a neglect of these important factors in investigations on natural control.

After distinguishing the two groups of factors mentioned above, I went on to examine the effect of the disappearance of factors of both types from controlling complexes made up in various ways. I concluded, in a general way, that the effect produced by the disappearance of general factors from a controlling complex is a *minimum* while the effect of the disappearance of individualized factors is a *maximum*. Finally I pointed out that though a considerable reduction in apparent mortality has in some cases very little effect on the total mortality yet the difference may have serious consequences, since a very slight increase in reproductive rate may rapidly produce a serious outbreak.

In 1945 H. A. Bess[5] returned to this subject in a paper entitled "A Measure of the Influence of Natural Mortality Factors on Insect Survival". In this paper Bess does not always express himself very clearly; however, it does appear that he considers himself to be professing views quite different from those I advanced in my 1928 paper. There is in fact a strong suggestion that both his methods and his conclusions are different.

More recently, the methods developed by Howard & Fiske, myself and Bess, have been utilized by Canadian forest entomologists, notably by Morris and Miller, in studies on the natural control of certain forest insects, particularly the Spruce Budworm. In his latest paper Miller[6] mentions the criticism of Bess

[4]J. econom. Ent., 28, 873-98. 1935.
[5]Ann. Ent. Soc. Amer. 38: 472-481. 1945.
[6]Can. Journ. Zool., 33: 5-17. 1955.

and summarises it by saying that in the view of that author, estimates should be based on the survival (adult) population rather than the initial population, which I, like my predecessors, took as a basis for calculating real mortality. The remarks of Miller suggest that he is not entirely clear about the significance of the criticisms made by Bess. Therefore, and since the calculations in question have now assumed some importance in field work it seemed worth while examining these criticisms so as to determine what difference, if any, there really is, between the methods and conclusions of Bess and mine.

The calculations of Bess are entirely arithmetical. The formulae I developed are algebraical and thus state the position in general, rather than in particular terms and lead to general conclusions. I propose therefore to take the general formulae of my 1928 paper and apply them to the calculations made by Bess. If these general formulae lead to the arithmetical conclusions of Bess then we must be basically in agreement. If not, then the principles and results of Bess may well be radically be different from mine. An examination of the detailed criticisms made by Bess can best be deferred until the fundamental structure of the argument has been examined.

Let us suppose we have a population passing through a series of stages—for example egg, larva, pupa and adult—that the proportion of eggs killed by a general mortality factor is (a) the proportion of larvae killed is (b) the proportion of pupae killed is (c) and the proportion of adults killed is (d): these proportions being taken each on a sample of individuals taken in the stage in question and calculated simply on that sample. In that case the total mortality in the population present at the beginning of the life cycle destroyed by all the factors taken together can be represented by the equation

$M = a + (1 - a)b + (1 - a)\ (1 - b)c$ etc. as in the 1928 paper . . . . . (1)

M being the proportional mortality for the whole population, 1-M will be the proportional survival and $\frac{M}{1 - M}$ will be the mortality survival ratio.

If we represent by the symbols A, B, C and D the fractions of the total initial population destroyed by each of the factors, F 1, F 2, F 3, F 4 etc. considered, the values of A, B, C and D will of course be as follows

$A = a$
$B = (1 - a)b$
$C = (1 - a)\ (1 - b)c$
$D = (1 - a)\ (1 - b)\ (1 - c)d$

Calling A, B, C, D, etc., the real destruction and a, b, c, d, etc., the apparent destruction the difference between the two will be evident from the following table:

Factor	App. destr.	Real destr.
F 1	a	a
F 2	b	$(1 - a)b$
F 3	c	$(1 - a)\ (1 - b)c$
F 4	d	$(1 - a)\ (1 - b)\ (1 - c)d$

Taking a numerical example, suppose that the four factors considered destroy each 10 per cent.–0.1 of the population present at the time of their action. The real fractions of the total population destroyed by each of them will be

F 1	0.1	or	10.0 %
F 2	0.09	or	9.0 %
F 3	0.081	or	8.1 %
F 4	0.0729	or	7.29%
Total	0.3439	or	34.39%

If 50 per cent of the available population were destroyed by each of these factors we should have as the real destruction

F 1	0.5	or	50.0 %
F 2	0.25	or	25.0 %
F 3	0.125	or	12.5 %
F 4	0.0625	or	6.25%
Total	0.9375	or	93.75%

The difference between apparent and real destructions effected by a given factor may thus be enormous.

Since the proportional or fractional mortality in the successive stages is A, B, C and D the survival in these stages will be (1 - a), (1 - b), (1 - c) and (1 - d). The mortality survival ratios will therefore be

$$\frac{a}{1-a}, \frac{b}{1-b}, \frac{c}{1-c}, \frac{d}{1-d}.$$

The real mortality, after all factors have operated will be, as already shown

$$M = a + (1 - a)\, b + (1 - a)\,(1 - b)\, c + (1 - a)\,(1 - b)\,(1 - c)d$$

which can be simplified to

$$M = 1 - (1 - a)\,(1 - b)\,(1 - c)\,(1 - d) \qquad (2)$$

and since survival = (1 - M), the M/S ratio is

$$M/S = \frac{1 - (1 - a)\,(1 - b)\,(1 - c)\,(1 - d)}{(1 - a)\,(1 - b)\,(1 - c)\,(1 - d)} \qquad (3)$$

This can be extended to any number of factors and any combination of ratios can be readily found by inserting the apparent mortalities for those considered and giving the others a zero value. An advantage of the method is that it gives, as a step toward the M/S ratio, the real mortality for the factors considered.

Bess gives a method for the combination of mortality survival ratios. In Table II of his paper, he lists 5 successive stages in which the apparent mortalities are respectively, 60%, 20%, 80%, 95% and 60%. The mortality survival ratios will therefore be 1.5, 0.25, 4.0, 19.0 and 1.5. Designating these as A, B, C, D and E, Bess states, that egg mortality plus first larval mortality equals A + B + AB = 2.125; egg mortality plus pupal mortality equals A + E + AE = 5.25; egg plus first larval plus pupal mortality equals 2.125 + 1.50 + 3.1875 = 6.8125. Bess actually calls these values "mortalities" though they really are mortality/survival ratios. His explanation of the summation process is inadequate. The substitution of figures for symbols in the last example conceals the complexity of the operation. The mortality survival ratio for the series is in fact obtained as follows:—

$$A + B + AB = K$$
$$K + C + KC = L$$
$$L + D + LD = M$$
$$M + E + ME = M/S$$

The values obtained by Bess in his example can be readily obtained by using equation (3).

After these preliminary remarks, the methods and main points produced by Bess may be considered. It is not easy to evaluate these because the remarks of Bess are at several points confused and inconsistent; and the objections he makes are not clearly formulated.

His purpose, says Bess, is "to point out why percentages of mortality are inadequate as measures of the reduction value of control factors and to present

a convenient measure for appraising and comparing the effects of different mortality factors". "The *reduction* produced by a mortality factor", he says further, "is the influence of the mortality effected by that factor during the development of the progeny from the egg to the adult stage." What Bess means by "influence" is not clear. He cites the view of Nicholson and Smith, that "If an attempt is made to assess the relative importance of the various factors known to influence a population, no reliance whatever must be placed upon the proportion of animals destroyed by each. Instead, we must find which of the factors are influenced, and how readily they are influenced, by changes in the density of animals". What Nicholson meant by this remark is quite clear but it has no connection with the results of Bess, whose data on controlling factors does not indicate whether or how they are influenced by the density of the insects on which they operate.

Bess then points out that the insects that escape death are the ones that are important from the standpoint of potential increase; and that percentages of mortality do not clearly show the relative influence of different degrees of mortality in reducing the number of survivors. These points are obvious. The economic effect of a pest depends, other things being equal, on its density. To reduce a large population per unit of area to a fixed level below economic damage, requires a higher percentage kill than to reduce a small population to the same level.

To illustrate his idea, Bess gives an example in regard to insecticides: of 1000 insects, insecticide A killed 500 or 50%; insecticide B, 900 or 90%; A plus C, 550 or 55%; B plus D, 950 or 95%. Thus, says Bess, both C and D killed 50 or 5% but C reduced the survival population only 1/10, while D reduced it by half. Therefore, says Bess, the addition of D was relatively more effective than the addition of C though the increase in the mortality was 5% or 50 insects in each case. But this simply means that with the population of 500, left by A, 5% kill is less effective than with the population of 100 left by B. To bring A down to 50, C would have to kill 450 or 90%. D is not really more effective than C. A better result is obtained because B is more effective than A.

In order to keep this real situation in focus, I actually began my discussion (1928, l.c., p. 98), by postulating a specific density and considering what percentage destruction would be required to produce stability. Howard and Fiske followed the same line of thought. Nowhere is there a suggestion that percentage destruction has always the same significance, irrespective of population density. If certain numerical examples had been selected this false impression might have been given. The basic idea of using symbols instead of numbers is, by stating the general case, to include all the possibilities.

Bess now proceeds to consider the use of the mortality/survival ratio. It represents, he says, the relative reduction in the survival population produced by the mortality; and indicates the reduction per individual survivor. To elucidate this, suppose the M/S ratio $= .6/.4 = 1.5$. This means that "the relative reduction in the survival population" is 1.5. Actually, 40 of 100 individuals survive. For each individual surviving, 1.5 or 60 in all have been eliminated. If the mortality survival ratio is multiplied by 100 and expressed as a percentage, it would represent the percent increase in the survival population which was prevented by the mortality. Certainly, $1.5 \times 100 = 150$. Since 40 survived instead of 100, the survival population would have been 150% of what is was with the 60% mortality.

These descriptions seem unnecessarily cryptic. If the mortality is 60%, that

means that of 100 individuals in a unit of area, 40 have survived. This is the essential fact. What it signifies from the economic standpoint depends on points not yet considered; the density at which economic damage occurs; the reproductive rate of the survivors etc., etc. The mortality survival ratio is after all merely a numerical relation between sections of a population not yet described in relationship to damage.

Bess cites the case of 2 similar fields, each apparently containing 50,000 insects per acre. Of these, one receives insecticidal treatment. In the field treated, 5,000 insects remain, while 50,000 are found in the untreated field. The mortality survival ratio in the treated field is 9, "which is the relative reduction in the survival population attributable to that mortality". However, this figure of 9 is not particularly illuminating from the economic standpoint, where the important point is the number of individuals remaining, related to the area in which they are found. Under certain circumstances, the elimination of 45,000 out of 50,000 might be satisfactory whether expressed as a percentage or as a mortality survival ratio, but in others it might be of no importance.

In Table II of his paper, Bess gives M/S ratios and numerical reductions in the adult population attributable to each mortality factor, in a case where the apparent mortalities in 5 stages of an insect with an initial population of 100,000 are 60%, 20%, 80%, 95% and 60%. He first calculates the M/S ratios and then, to obtain the numerical reduction in the adult stage for each factor, he multiplies the final population by each mortality survival ratio, which gives: 192, 32, 512, 2432, 192.

In this case the total mortality determined by all factors is given by equation (2) and is

99,872, the survival being 128.

Taking the equation (2) with three factors, we have, as the total mortality and survival

$M_1 = 1 - (1 - a)\ \ 1 - b)\ (1 - c)$

$S_1 = (1 - a)\ \ 1 - b)\ (1 - c)$

If one factor, for example, a, disappears, we have, at least for general factors, mortality and survival,

$M_2 = 1 - (1 - b)\ (1 - c)$

$S_2 = (1 - b)\ (1 - c)$

Subtracting M_2 from M_1 we get the irreplaceable mortality for factor a: i.e., the part of the total mortality that could not occur without it, in spite of the action of subsequent factors.

Thus, if we have 3 factors, giving apparent mortalities of .6, .5, and .8, the total mortality will be

$M_1 = 1 - .4 \times .5 \times .2 = .96$ and

$S_1 = .04$

If *a* disappears, we have,

$M_2 = 1 - .5 \times .2 = .90$

$S_2 = .10$

The irreplaceable mortality for factor a is

$IMa = M_1 - M_2$

$= a\ (1 - b)\ (1 - c)$

$= .06$

The survivors after the action of all factors are

$S_1 = (1 - a)\ (1 - b)\ (1 - c)$ and the irreplaceable mortality

$IMa = a\ (1 - b)\ (1 - c)$

$$\therefore \frac{IMa}{S_1} = \frac{a}{(1 - a)} \text{ and } IMa = \frac{S_1 a}{(1 - a)}$$

so that the irreplaceable mortality for a can be obtained by multiplying the number of survivors after the action of all the factors a, b, and c, by the mortality survival ratio for a

$IMa = .04 \times 1.5 = .06$, as before.

This is the method adopted by Bess in Table II. As I have shown, it can be derived from the fundamental equations given above.

It may be noted that the method of calculating the irreplaceable mortality for a factor was given in the 1928 paper, p. 101, under no. 4 and exemplified on p 102; but the relation noted by Bess was not explicitly brought out.

In his table II Bess calls the irreplaceable mortality the "numerical reduction in the adult population attributable to each mortality".

This statement is misleading. In fact, the egg parasites killed 60% or 60,000 eggs, and if no other factor had acted, this would have been the irreplaceable mortality for egg parasites. It is true that if they had disappeared and the following factors had acted as shown, then all but 192 of the 100,000 insects would have been killed. But they did not disappear and did, in reality kill 60,000 insects in the egg stage.

On page 476 of his paper, Bess again touches on the question of the indispensible or irreplaceable mortality. He says that I presented the "indispensable" mortality as a fraction of the original population "and used it to more or less minimize the effects of any one factor, to show that . . . the factors which disappear are *to a large extent automatically replaced by those which follow them.*" He then cites my conclusion that ". . . one may thus have relatively large fluctuations in the apparent mortality by the controlling factors without any very noticeable change in the progress of events." "This viewpoint", says Bess, "is entirely different from that which is the basis of this paper, which suggests that fluctuations in the apparent mortality may have a tremendous effect on the survival population."

Two comments on these remarks seem necessary. The first is, that since, as I have shown, all the arithmetical examples given by Bess are simply particular cases of the general propositions given in my formulae, there should not really be any basic disagreement, though there may be differences of appreciation or viewpoint in regard to the same fundamental facts. Thus to take the example in Bess' table II, I would say that since the disappearance of parasites killing 60,000 out of a population of 100,000 results in the survival of 192 more adults, or a population of 320 instead of 128, this great change in apparent mortality has had little effect on the progress of events. If we say that the population is now 2½ times what it would have been with the parasites, the change may look more impressive; but if it occurs below the threshold of economic damage it may attract no notice. The second comment is that the quotation given by Bess referred in my paper, to the case of *general factors*, where the effect produced by the disappearance of a factor is a *minimum.* The case considered above involves *individualized factors*, where the effect of the disappearance of the factor is a *maximum.*

We now come to Tables IV and V. For convenience in discussion, these are reproduced below.

TABLE IV

The Estimated Effect of Different Groups of Parasites on Survival to the Adult Stage.

Stage	Per Cent of Population Parasitized by Parasites of.....				Mortality/Survival Ratios for the Parasites of.....			
	Group A	Group B	Group C	Total	Group A	Group B	Group C	Total
Egg.....	57.9	.0	11.1	60	1.375	0	0.125	1.500
1st larval.....	11.1	5.8	5.9	20	0.125	0.062	0.063	0.250
2nd larval.....	42.9	20.0	75.0	80	0.751	0.250	3.000	4.000
3rd larval.....	37.5	94.7	28.6	95	0.600	18.000	0.400	19.000
Pupal.....	11.1	27.3	50.0	60	0.125	0.375	1.000	1.500
Total reduction effect....				99.872	7.416	33.681	12.394	780.250

TABLE V

The Estimated Effect of Different Mortality Factors on Survival of the Adult Stage.

Stage	Population	Per Cent Mortality by			Proportionate Part of Total Ratio				Total Ratio
		Parasites	Predators	Diseases	Total	Parasites	Predators	Diseases	
Egg.....	100,000	55	0	5	60	1.375	0	0.125	1.500
1st larval...	40,000	10	5	5	20	0.125	0.062	0.063	0.250
2nd larval..	32,000	15	5	60	80	0.750	0.250	3.000	4.000
3rd larval..	6,400	3	90	2	95	0.600	18.000	0.400	19.000
Pupal.....	320	5	15	40	60	0.125	0.375	1.000	1.500
Adult.....	128	—	—	—	—	—	—	—	—
					99.872	7.416	33.681	12.394	780.250

Each of these tables presents a debatable peculiarity which does not seem to be fully elucidated in the text. For reasons that will appear a little later, Table V must be considered first.

Table V gives the mortality produced in the eggs of a host insect by parasites as 55% and by diseases as 5%. The total mortality is given as 60% so that there is clearly no overlapping. To me it appears that since the egg parasite kills 55% of the eggs and leaves 45%, the M/S ratio is 1.22 approximately. If there were no other cause of mortality, this is certainly what it would be. Similarly, the M/S ratio for disease would be 5/95 or .052 approximately. However, if the

factors are independent and do not act in a sequence, their total mortality is 60%, the survival after they have both acted is 40 and the M/S ratio is 1.50. We can then say that 1.375 of this is in a sense, attributable to the parasites and 0.125 attributable to the diseases but it is hard to say what is gained by this method of describing the facts. In fact what Bess does is to split the mortality from one factor, saying that 55 individuals of parasite A killed each 1 host, 5 individuals of the same species also killed one; in that case 1.375 and 0.125 are the proportionate shares of the M/S ratio. If two species are involved a simple comparison between the numbers present is, it seems, more useful than the comparison of ratios. In his comments on Table V, Bess suggests, as a justification of his procedure, two possibilities: the first is that the parasites lay eggs in about the same percentage of the eggs classed as diseased as in those classed as non-diseased; while disease is found in the same percentage of parasitized and unparasitized eggs: the second is that the parasites avoid or tend to avoid diseased eggs, while disease is less successful in parasitized than in unparasitized eggs.

Since exact figures are used by Bess, the hypotheses they exemplify should also be exact; and such qualifying statements as "about the same percentage" and "tend to avoid" must not be made.

If the parasites lay eggs in the same proportion in parasitized and unparasitized eggs, then, if they attack 30% of the eggs they will get 30% of each category; if the disease is distributed in the same way among parasitized and unparasitized eggs, and 40% of the eggs are attacked, then 40% of each category will be diseased.

Since we have 60 healthy eggs and 40 diseased eggs, the parasite will attack 18 of the first category and 12 of the second. If the parasite dominates, we shall have 30 eggs killed by parasites and 28 killed by disease, the total kill being 58. We can also say that there are 70 unparasitized eggs and 30 parasitized and that the disease attacks 40% of each which gives 28 diseased eggs in the first category and 12 in the second category. If the parasite dominates then 30 eggs will be killed by parasites and 28 by disease, as before. If the disease dominates, then only 18 will be killed by parasites while 40 will be killed by disease in both cases. This leads to the same result as if the factors acted in a sequence.

If the parasite avoids diseased eggs and the disease avoids parasitized eggs, then if the attack remains as stated, the parasite will kill 30% and the disease will kill 40%, the total kill being then 70%.

The second supposition made by Bess agrees with Table V, in which the percentages are added but the first supposition does not. Neither supposition agrees with Table IV.

In Table IV a different procedure is adopted. Here the mortality/survival ratio is taken as the relation between the percentage mortality due to a given species and the percentage that survives its attack. The ratios for the various factors are the same as in Table V and so, for the egg parasite of Group A we must have

$$\frac{1 - a}{a} = 1.375$$

$$a = 1.375 - 1.375a$$

$$2.375a = 1.375$$

$$a = 0.579 \text{ or } 57.9\%$$

For the egg parasite of Group C, we must have

$$\frac{1 - c}{c} = 0.125$$

$$c = 11.1$$

The total percentage of egg parasitism is given as 60%. The parasitisms, when added, total 69.0%; in the next horizontal row they add up to 22.8% but are totalled as 20%; in the third row they add up to 137.9% but are totalled as 80%; in the fourth, add up to 160.8 but are totalled as 95%; in the last, add up to 88.4 but the total is 60%.

These combinations of percentages seem to follow no particular law. The added totals have always a different relation to the total adopted. The percentages do not combine as in a sequence; if they did, we should have, for the total of egg parasitism.

$$.579 + (1 - .579)\ .111$$
$$= .6257 \text{ or } 62.6 \text{ approximately}$$

Bess says (p. 479) that the parasites attacked the hosts "indiscriminately"; but this means "at random"; 69 parasites distributed among 100 hosts would not, however, give 60% parasitism but

$$100\ (1 - e^{-.69})$$
$$= 50\ \% \text{ approximately}$$

The only discernable principle seems to be to obtain the same ratios as in Table V, while changing the character of the mortality/survival ratio. There is of course, nothing intrinsically impossible in the suppositions made. A parasitism of 57.9% might combine with a disease attack of 11.1% so that the total kill would be 60%; and this is quite possible for the other combinations, no matter how different they are. The difficulty arises from the fact that the only basic principle involved seems to be the desire of Bess to reach the same numerical mortality survival ratios starting from two different definitions of the mortality survival ratio itself.

In what has preceded, I have dealt mainly with the direct or indirect criticisms of my 1928 treatment made by Bess and with certain special difficulties presented by his paper.

However, a more fundamental objection which I have already indicated, can be made to his treatment. This applies to some extent to the sketch given by Howard and Fiske in their 1912 Bulletin. This is, that in all his tables, Bess, though referring exclusively to parasites, predators and diseases, that is, to individualised or dependent factors, adopts a model that applies to general or independent factors. The postulate implicit in his tables, is that if one control factor disappears, the following factor will destroy the same *proportion* of organisms as it did when the preceding factor was present and therefore had reduced the population; the destructive power of the general factor being independent of the numerical status of the host. This can hardly apply to a parasite or predator. Suppose, for example, that in an area containing 1000 eggs of an insect, a general factor sometimes kills 50%. After this, egg parasites arrive on the scene. If there are 10 parasites, laying 10 eggs each and the accessibility of the eggs is sufficient and constant, there will be 10% parasitism when the general factor does not act, and 20% parasitism when it does act. These are apparent parasitisms; but the real mortality with respect to the initial population will remain constant at the figure of 100 or 10%. Suppose control is effected entirely by a series of such factors, each killing 100 individuals, then clearly the dis-

appearance of any one will cause the real mortality = MP, to fall by 10%. This fall will cause a drop in the apparent mortality from the succeeding factors; and these factors will not compensate, as do the general factors, for the disappearance of their predecessors. Adopting these postulates, the effect of the disappearance of factors of the two types can readily be calculated. If we take a case where factors F1, F3, F5 and F7 are general factors, while F2, F4, and F6 are individualized factors; the proportional apparent mortalities for the factors of the first group being 0.5, 0.6, 0.8, and 0.8, while the numerical mortalities for those of the second group are 100, 60 and 10, and the initial population of the pest, 1000, then the total kill after the operation of all factors will be 998 with 2 survivors. If the individualised factors had not operated, the kill would be 992. The fall in the mortality is therefore only 6 or 0.6%, although the individualised factors had killed 170 specimens and had produced an apparent mortality of 107.5% and a real mortality of 17.0%. This result is in conformity with the conclusions of the 1928 paper. It is true that the residual population is now 4 times what it was when the individualised factors operated, but whether this or the other figures mentioned, are economically significant or not, cannot be determined *a priori*. What does seem clear is that the change is much less than one would expect it to be, considering the apparent mortality produced by the factors that have ceased to operate.

The example given on p. 104 of my 1928 paper is incorrectly worked out, for all the factors are treated as independent or general factors. The total mortality, calculated from equation (2) works out at 98.06 which is the approximate figure given. If the so-called individualised factors are eliminated, the mortality becomes 93.99 and this is the value of D given by the equation on p. 105, inserting the apparent mortalities given in the table on p. 104. It is given in the text as 94.0% approximately.

The algebraical treatment of cases involving the two types of factors in my 1928 paper is unnecessarily cumbersome because it was developed from the general equation (1) and therefore gives a very complex representation of the mortality values of the individualised factors. These are in fact represented by the expressions for real mortality in the table on p. 101 of my paper. The equations can be simplified but this itself is a laborious process.

If we say that the proportional *apparent* mortalities for 3 independent or general factors F1, F3 and F5 are a, b and c, the proportional *real* mortalities calculated with respect to the *original population*, for 2 dependent or individualised factors, F2 and F4, are e and f, while the population is P; the number surviving after the operation of all factors will be

$$NS = P\ [(1-a)-e]\ (1-b) - f\ (1-c)$$

If we put e = f = o, which means that the dependent factors disappear, we have

$$NS = P\ (1 - a)\ (1 - b)\ (1 - c)$$

which agrees with our original formulation.

If we put a=b=c=o, which means that the independent or general factors cease to act, we have

$$NS = P\{1 - (e + f)\}$$

which corresponds with the method of my 1928 paper p. 101.

Putting a=b=c=.2; e=f=.3; P=100,

we get NS=8, which is verified by an arithmetic check. The method of expanding the expression to include any number of factors will be evident from the equation itself.

The postulate that the individualized factor always destroys the same number of individual organisms, is of course an ultra-simplification. It has as a basis the fact that reproductive rates are specific characters, subject of course to the variation observed in all such characters, but attached to a definable specific nature. Under certain circumstances, the rate is no doubt affected by the density of the population of the prey; but above a certain limit, host density may not greatly influence the rate. In passing from the simple formulation to the facts many complications come into the picture. It was once supposed that parasites oviposit at random but it is now known that some possess a remarkable power of selecting unparasitized hosts, avoiding even a host that contains the egg of another parasite. In a controlling complex the alteration of one factor may affect the controlling value of other factors. In fact, all we can reasonably hope is that formulations such as those discussed here may provide convenient patterns of thought, serving for the provisional integration of data and indicating lines of research.

Differences in the Pupae of *Feralia comstocki* Grt. and *F. jocosa* (Gn.) (Lepidoptera: Noctuidae)[1]

By D. A. Ross[2]

Difficulties experienced in rearing *Feralia* spp. beyond the pupal stage, and inability to distinguish species in the immature forms, has led to a study of their larvae and pupae. So far no specific differences have been observed in the larvae but progress has been made in the identification of *Feralia* in the pupal stage.

During the past two years we have succeeded in rearing moths of *Feralia jocosa* Grt. from the region between latitudes 49 and 52 degrees, and *F. comstocki* (Gn.) from between latitudes 50 and 54 degrees in the interior of British Columbia. The host of 10 *F. jocosa* specimens was *Pseudotsuga taxifolia.* Hosts of 16 *F. comstocki* specimens were *Pseudotsuga taxifolia* (6), *Tsuga heterophylla* (4), *Abies lasiocarpa* (3), *Picea glauca* (2), *P. engelmanni* (1), Thus a good series of pupae of both species have been available for study. Unfortunately, we have no pupae of *F. deceptiva*, a British Columbia coastal species.

The abdomen only was studied carefully for specific differences, the greatest attention being concentrated on its chaetotaxy. There are a few minute setae on the central moveable abdominal segments of *Feralia* pupae. Post-spiracular seta iv? (Dyar and Forbes) and subspiracular seta vi? occur on the pupae of *Feralia comstocki* and *F. jocosa;* apparently there is no relative difference in their location in these species.

The only reliable specific distinguishing character is the number of hooks on the terminal abdominal segment. *Feralia jocosa* (Fig. 2) has two stout slightly hooked cremastral spines; *F. comstocki* (Fig. 1) has, in addition to two stout strongly hooked cremastral spines, a similar pair of hooked spines. An examination of 15 to 20 pupae of each species has demonstrated the reliability of this character in separating these two species of *Feralia.*

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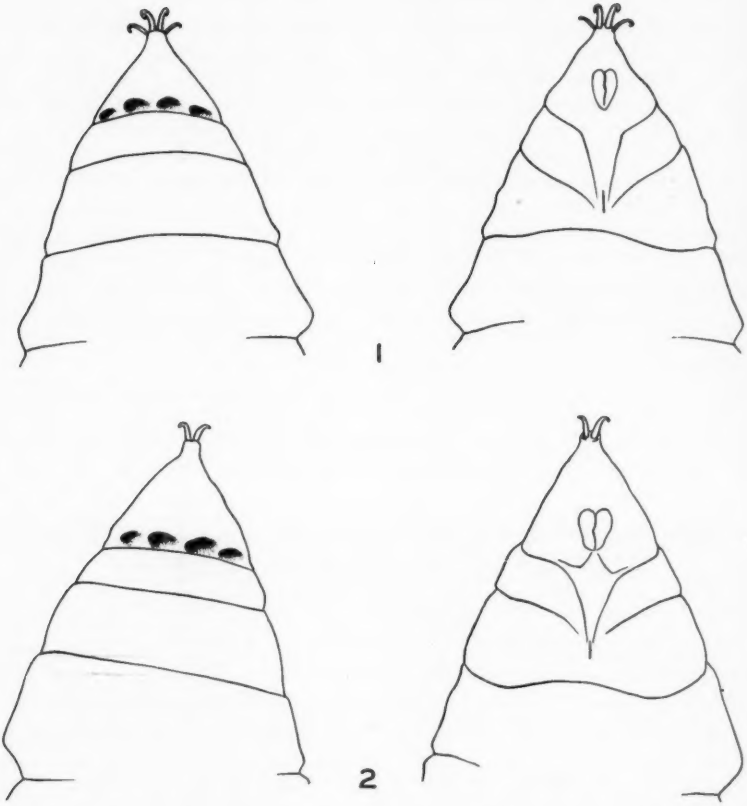

Terminal abdominal segments of male *Feralia* pupae (dorsal and ventral aspects)
Fig. 1. *F. comstocki* Grt. Fig. 2. *F. jocosa* (Gn.)

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ERRATUM

In line 4 of first paragraph, p. 210, Vol. 87, for "New England" read "New Zealand".

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